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MORPHOLOGY AND DEVELOPMENT OF *NOSEMA NOTABILIS* KUDO

Parasitic in *Sphaerospora polymorpha* Davis,
A Parasite of *Opsanus tau* and *O. beta*

WITH 12 PLATES AND 7 TEXT FIGURES

BY

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CONTENTS

I. INTRODUCTION

OF A NUMBER of cases of hyperparasitism reported in literature, in which a parasitic protozoan is parasitized by another protozoan, four microsporidians have been reported to occur as hyperparasites. Lutz and Splendore (1908) noticed the occurrence of *Nosema balantidii* in *Balantidium* sp., a ciliate, inhabiting the colon of *Bufo marinus* in Brazil. The spores of this microsporidian, which were found scattered, or in groups of four or eight, in the cytosome of the host ciliate, were pyriform and measured 2-5 μ by 1-3 μ. Since these authors failed to prove the presence of the polar filament in the spore, the microsporidian nature of the organism is open to question.

Léger and Duboscq (1909) reported the occurrence of *Nosema frenzelinae* in the cytosome of *Frenzelina conformis*, a cephaline gregarine, which was parasitic in the intestine of a crab, *Pachygrapsus marmoratus*, at Cavaliere, France. The same two authors (1909a) found another microsporidian, *Perezia lankesteriae*, in the cytosome of *Lankesteria ascidiae*, an acephaline gregarine, parasitic in the intestine of a tunicate, *Ciona intestinalis*, at Cette, France. In 1919, Stempell observed *Nosema marionis* (Thélohan) in the cytosome of the trophozoites of *Ceratomyxa coris*, a myxosporidian, inhabiting the gall bladder of *Coris julis* and *C. giofredi* from French waters. This microsporidian had previously been noticed by Thélohan (1895) who, however, believed that the whole of the trophozoites were of a microsporidian, consequently, he considered the organism a coelozoic microsporidian, and named it *Glugea marionis*.

Recently I have observed the fifth case of microsporidian infection in a parasitic protozoan. In the summer of 1939, while examining the fishes of Chesapeake Bay for protozoan parasites at Solomons Island, Maryland, I discovered that the trophozoites of the very common myxosporidian *Sphaerospora polymorpha* Davis, inhabiting the urinary bladder of the toadfish, *Opsanus tau*, were frequently infected by a microsporidian for which the name *Nosema notabilis* was proposed (Kudo, 1939). It became known soon afterwards that this microsporidian attacks only the myxosporidian and does not infect any of the host fish cells. The infected myxosporidian trophozoites showed a cytological change characteristic of microsporidian infection. It therefore appeared certain that the microsporidian was a true and exclusive parasite of the myxosporidian. Since the microsporidian develops within small and isolated myxosporidian trophozoites, it seemed to present ideal material for me to renew work on this group of Protozoa in which I have been interested since 1910. In working out the morphology and development of *Nosema notabilis*, it became necessary to carry on a similar study of the host myxosporidian. For this purpose the toadfishes of Maryland and Florida were studied

here at Urbana, Illinois. Although the study did not reveal the complete life cycles of these two cnidosporidians, it brought to light certain important facts and new information which are here summarized.

Since this monograph was accepted for publication in December, 1941, data which appeared in papers after that time are not included.

II. MATERIAL AND METHODS

THE UNIQUE association of the two cnidosporidians under consideration was first discovered at Chesapeake Biological Laboratory, Solomons Island, Maryland, in July, 1939. During that summer the toadfish, *Opsanus tau*, were caught with hook and line or with seines in the vicinity of the Laboratory. During late fall and winter when the fish remained buried in mud, Mr. D. H. Wallace of the Laboratory used oyster tongues to good advantage. This confirms the earlier observations of Ayres (1842), Storer (1885), and others, as quoted by Gudger (1910), to the effect that the toadfish move to deeper water and bury themselves in the mud during the colder months. I am greatly indebted to Mr. Wallace for the collection and preservation of the material during October and December, 1939. In all, thirty-two fishes, varying from 10 to 25 cm in length, were studied from the Chesapeake Bay at Solomons Island.

During December, 1940, and January to March, 1941, fifty *Opsanus beta*,[1] 8 to 28 cm long, were obtained from Lemon Bay, Englewood, Florida. These fishes were received in shipping tanks on different dates. All arrived alive at Urbana, Illinois, except fifteen which apparently had died during the period of transportation. The living fishes were kept under observation in aquaria for up to three weeks from the day of their arrival.

For observation of living organisms, Nemeczek's (1926) hanging drop preparations, which I have been advocating for several years for the study of Myxosporidia, were made with the urine in which the organisms lived. Numerous cover-glass smears of various thickness were prepared by spreading drops of urine and scrapings of the bladder epithelium. The myxosporidian trophozoites are mostly attached to the bladder epithelium, so that smears that were made from empty bladders showed abundant and rich material. Many bladders, together with the ureters and portions of the kidney, were fixed in toto and serially sectioned 2-8 μ thick in paraffin.

As fixatives, Schaudinn's, Carnoy's, Bouin's, and Flemming's (strong) solutions were used as in previous works. Staining was carried on with Heidenhain's iron haematoxylin or Giemsa's solution in addition to

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[1]Schultz and Reid (1937) consider that the toadfishes from the west coast of Florida are distinguishable from *O. tau*. I am indebted to Dr. C. L. Hubbs, of the University of Michigan, for information concerning these fishes.

Feulgen's nucleal reaction. The following combinations gave the best results: Carnoy, Schaudinn, Flemming, or Bouin and Heidenhain; Carnoy or Schaudinn and Giemsa or Feulgen.

The extrusion of the polar filaments of the spores of *Sphaerospora polymorpha* was easily accomplished as before by addition of potassium hydrate or hydrogen peroxide, or under mechanical pressure (Kudo, 1918, 1920a). The spores of *Nosema notabilis* were comparatively much fewer than in the other Microsporidia which I studied; for example, *Nosema bombycis* (Kudo, 1913, 1916) or various microsporidians of mosquito larvae (Kudo, 1921a, 1924, 1925, etc.). The methods employed successfully previously were unsatisfactory for observation under the dark-field microscope of the species under consideration. Hydrogen peroxide treatment of the spores brought about the filament extrusion in the usual manner, but it required a great deal of time to recover in dark field the affected spores in a highly agitated medium. However, by using a changeable condensor and apochromatic objective 20, it was possible to detect a few fresh spores in a very thin smear preparation in bright field. A dissecting needle with a bent tip was pressed down on the upper surface of the cover-glass while under observation, and when an optimum amount of mechanical pressure was thus applied, the polar filaments were extruded from the spores, which now became less refractile and more rounded. The extruded polar filaments can hardly be recognized in bright field (fig. 167), but are easily observed by quickly changing the field from bright to dark. The same manipulation was carried on equally successfully with an apochromatic oil immersion objective 60 with a built-in diaphragm, in which case the objective was raised at the time of the application of the needle to the cover-glass (figs. 166, 167). For permanent preparations of the spores of *Nosema notabilis* with their extruded filaments, I obtained satisfactory results by using the methods previously employed (Kudo, 1913, 1918, 1921).

III. URINARY SYSTEM OF *OPSANUS TAU* AND *O. BETA*

Since the two cnidosporidians with which the present paper deals have so far been found only in the urinary bladder of *Opsanus tau* and *O. beta*, it was necessary to obtain fuller information than that available in literature on the anatomy of the system in these host fishes. Comparative examinations indicate that the system in the two species of toadfish possesses the same morphological characteristics.

The relatively large compact kidney is a paired organ, extending over a large area on the dorsal surface of the body cavity. The anterior two-

fifths are separated into the right and left lobe, while the remaining portion is fused into a slender median band which tapers to a fine strand at its posterior end. In a fish 10 cm long, the kidney was about 3 cm long, the anterior region of the two lobes 4-6 mm wide, and the posterior fused part 13-15 mm long by 1-3 mm wide. During the course of the study, serial sections of the kidneys of several fishes were carefully examined with expectation that certain stages in the development of the two cnidosporidians might occur in the kidney. The search ended in disappointment, but it revealed that the toadfish kidney contains no glomeruli, which condition had first been discovered by Marshall (1929).

From the dorso-lateral edges of the posterior portion of the kidney arise two ureters, which extend side by side along the median line of the body and open into the urinary bladder. The ureters vary from 5 to 10 mm in length in fishes 10 to 20 cm long, as measured between the posterior tip of the kidney and the points of attachment to the urinary bladder. The two ureters open independently into the bladder. In a female fish 12 cm long, which had been fixed with Carnoy's fluid and sectioned, the distance between the openings of the two ureters was 450 μ as seen in serial sections.

The urinary bladder is situated above the gonads, and, except in the posterior region, is without any tissue attaching it to the peritoneal membrane or viscera, being freely suspended in the body cavity. There is a sexual dimorphism with respect to the form and arrangement of the bladder. In the male fish, there are right and left horns or lobes which are connected with each other posteriorly (text fig. 1). In all fishes examined, the left horn contained far greater amounts of fluid than the right one. In a number of fishes, the left horn was fully distended and reached the anterior end of the body cavity, while the right horn appeared empty, narrow, and small, with a wrinkled wall. At first it was thought that prior to dissection, the right horn may have emptied its contents, which would result in its smaller size. But when fishes which have been dead a short time are opened, both horns of the bladder are usually not inflated, and here again the difference in dimensions between the larger left and smaller right horns is conspicuously noticeable. It appears certain, therefore, that the left horn is naturally much larger than the right one. The anterior region of the left horn in particular, appears occasionally to show a tendency to remain distended after the remaining part emptied its contents, due possibly to strong transverse muscles located in the bladder wall.

In a freshly sacrificed male fish, 13 cm long, the left horn was expanded and measured 3 cm long by 9 mm wide at the broadest point, while the right horn was 12 mm long by 4 mm wide. In another male fish, 22 cm long, examined about 48 hours after death, both horns were contracted. The left horn measured 28 mm long by 3 mm wide, and the
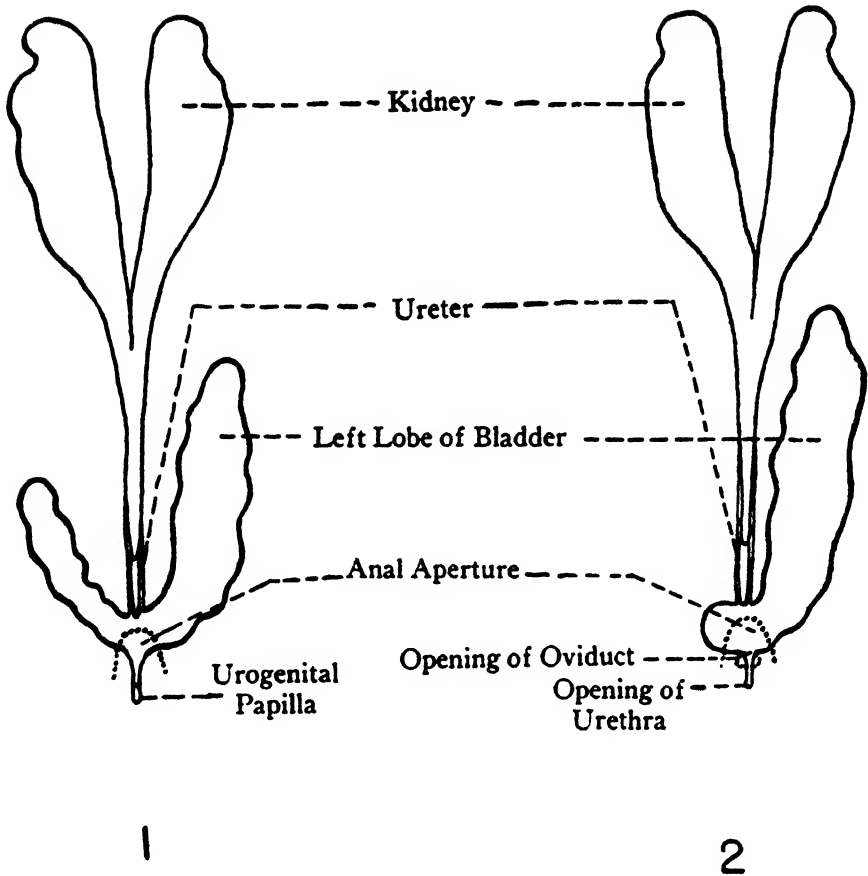
TEXT FIGS. 1-2.—Diagrams of the urinary system of the two species of Op-sanus, as seen from the ventral side; 1, male; 2, female.

right, 17 mm long by 1.5 mm wide. In a third male fish, 10.5 cm long, examined after death, the left horn was 13 mm long by 2 mm wide near its posterior end, while the right horn was 4 mm long by 1 mm wide.

In the female fish, the left horn is always conspicuously noticeable, but the right horn does not occur (text fig. 2). The left horn is similar in form and appearance to that of the male fish. In two female fishes, both 12 cm long, which died during transportation, the urinary bladder measured 20 mm long by 3 mm wide and 15 mm long by 4 mm wide. In a freshly sacrificed female fish, 15 cm long, the highly distended bladder, located above the left ovary, measured 33 mm long by 8 mm wide.

The urethra is a short tubule connecting the posterior end of the bladder with the urinary pore, which is located behind the opening of the oviduct and in turn opens posterior to the anal aperture. The urine or fluid content of the bladder is colorless and translucent. Its pH as measured by the calorimetric method averages 7.2.

These findings will now be compared with those of previous observers. The first observation on the urinary organ of the toadfish appears to have been made by Hyrtl (1851). Studying a female *Batrachus tau*, which was "5 Zoll" (about 12.7 cm) long, Hyrtl made the following observation: "Die Blase selbst liegt links vom linken Ovarium, hat 9 Linien Länge, und besteht aus einem hinteren 3 Linien weiten, und einem vorderen nur 2 Linien weiten Abschnitte. Die anderthalb Linien lange und feine Urethra mündet auf der hinteren Lefze der weiten Genitalöffnung." Hyrtl gave a figure (his pl. 14, fig. 3) which is reproduced here in text fig. 4. Thus the single-lobed condition of the urinary bladder of the female toadfish had correctly been observed by Hyrtl.
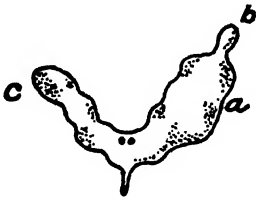
TEXT FIGS. 3-4.—Hyrtl's illustrations; 3, the urinary bladder of *Batrachus cryptocentrus:* a, "left flap of bladder," b, "diverticulum on its crown," c, "right, narrower and shorter flap"; 4, the urinary bladder of *Batrachus tau*, "composed of two unequally wide segments."

The same author examined a male *Batrachus cryptocentrus*, "6 Zoll" (about 15.2 cm) long, and described his findings as follows: "Zwei Ureteren treten in den Rücken einer asymmetrisch zweilappigen Blase, deren rechter Lappen schmäler und etwas langer als der linke ist. Beide Lappen sind sehr ansehnlich, und liegen an den entsprechenden Bauchwänden an. Der Linke ist noch überdiess an seinen gerundeten Scheitel mit einem 1½ Linien langen, engen Diverticulum versehen. Es findet sich nur eine einfache Urogenitalöffnung auf einer niedrigen und dünnen Papille am hinteren Afterrande." Hyrtl gave a figure (his pl. 14, fig. 2), which is reproduced here as text fig. 3. This figure does not bear out what he stated in the text, since in his explanation of this figure, Hyrtl stated that *a* indicated "linker Lappen der Blase," *b*, "Diverticulum an dessen Blase," and *c*, "rechter, schmälerer und kürzerer Scheitel." Thus his text statement based on one male fish is in discrepancy with the illustration, presumably taken from the same fish. If he erred in the text and was correct in the illustration concerning the right and left sides, my observation of the urinary system of the male Opsanus is in accord with that of the male *Batrachus cryptocentrus* as observed by Hyrtl.

Gudger (1910), in his studies on the habits and life history of the toadfish, gives photographs of the gonads and urinary bladder of *Opsanus tau* which are unfortunately indistinct in the copies I have examined. His fig. 1-A, a dorsal view of the male organs, appears to show the left horn of the bladder as longer and wider than the right. The sperm duct and urethra open independently according to Gudger, as he writes: "They [elongated glands] are confluent behind to form the sperm duct, which opens in the same place and manner as the oviduct." In the description of the ovary, Gudger stated that "in fig. 1 the anus is shown and to the left of it one of the paired halves of the urinary bladder." This leads me to think that Gudger observed paired lobes in the bladder of a female toadfish. His fig. 2, labelled "ventral aspect of living ovary," appears to be in reality a dorsal view, because the urinary bladder appears above the (left) ovary, and also judging from the erroneously placed label for fig. 1-C in which the anal aperture is visible. If this interpretation of Gudger's photographs is correct, there appears to be a single sac for the urinary bladder located close to the ovary in his photograph, and his observation agrees with my observation mentioned above.

Marshall (1929), who made a careful histological study of the kidney, makes the following statement: "The bladder is bi-lobed but the lobe on the right is usually very small in comparison with that on the left. The two lobes are in communication. The ureters pass up from the bladder on each lateral edge of the fused posterior portion of the kidney, and then disappear into the substance of the middle portion of the organ." He does not mention any difference in the form of the bladder between the male and female fishes. However, referring to Hyrtl's work quoted above, Marshall states that "his description of *Batrachus cryptocentrus* is evidently that of our toadfish rather than his account of *Batrachus tau;*" since the latter was a female fish, I am led to assume that Marshall did not recognize the sexual dimorphism in the urinary bladder of the toadfish *Opsanus tau.*

Because of its easy access and hardy nature, the toadfish has occasionally been used by physiologists for investigations on osmotic regulation, urine flow, diuresis, etc. For example, Graffin (1931) used *Opsanus tau* for his study on urine flow and diuresis. The fishes were collected in the vicinity of Baltimore, a short distance from Solomons Island where all toadfishes were found to be parasitized more or less heavily by *Sphaerospora polymorpha,* which in turn was infected to a varying degree by *Nosema notabilis.* It is assumed that the two cnidosporidians consume substances present in the urine, as well as in the bladder epithelium, for growth and reproduction. There is no way of estimating the amount of substances consumed by them and how much catabolic waste matter is excreted by them, but in a heavy infection, in which the bladder epithelium is completely covered by one to many layers of trophozoites of the

myxosporidian, the amount may be considered relatively large. The urine analysis of the toadfish, therefore, indicates in reality the sum-total of the excretion by the host fish into the bladder and of the catabolic products excreted by the two protozoans, less the material used by the latter organisms, and it obviously does not give the true picture of the urinary excretion of the toadfish itself.

IV. *SPHAEROSPORA POLYMORPHA* DAVIS

OCCURRENCE

As WAS STATED already, eighty-two toadfishes, varying in length from 8 to 30 cm, were examined during July, August, November, and December, 1939, December, 1940, and January to March, 1941. All the fishes harbored the myxosporidian in the urinary bladder in varying numbers. Even when the trophozoites or the spores could not be detected in fresh preparations, a small number of trophozoites attached to the bladder epithelium could be observed in section preparations. In the bladder of the majority of the fishes examined, the myxosporidian was abundantly present. Although numerous trophozoites were seen floating freely in the urine of the bladder (fig. 159), the majority were attached to the bladder epithelium; in fact, the inner surface of the bladder wall was completely or in part covered by trophozoites, which were arranged in so compact a fashion in a single layer that the organisms showed all possible angular forms (text fig. 5). In several fishes, the bladder wall was covered in places by several layers of trophozoites of various sizes of the myxosporidian (fig. 162). The present study reveals that this myxosporidian is represented by all stages throughout the year, except in spring in which no examination has so far been made.

Davis (1917), who discovered and described this myxosporidian, examined 11 *Opsanus tau* at Beaufort, North Carolina, in June and July, and found 9 harbored the organism abundantly. He stated: "The trophozoites are usually attached to the urinary epithelium which in badly infected fish may be almost entirely covered with them."

Of numerous Myxosporidia that are parasitic in the urinary bladder of various fishes (Kudo, 1920a), *Sphaerospora elegans* and *S. divergens* were found in both the renal tubules of the kidney and the bladder. In the case of *Myxidium lieberkühni*, the well-known species inhabiting the urinary bladder of species of Esox in North American and European waters, Debaisieux (1918) found that it invaded not only the bladder, but also the uriniferous tubules and even the glomeruli of the kidney, in which the organism produced cysts. *Sinuolinea dimorpha* was found by Davis (1916, 1917) in the urinary bladder and Wolffian ducts of *Cynoscion*

regalis. On the other hand, there appear to be a number of myxosporidians which inhabit the bladder only. For example, Auerbach (1909) found *Zschokkella hildae* only in the bladder of *Phycis blennioides, Gadus callarias,* and *G. virens* at Bergen, Norway.

Sphaerospora polymorpha appears to belong to the latter group in that it inhabits or passes its major portion of existence in the urinary bladder of the toadfish only. Repeated search in serial sections of the ureters and kidneys of several host fishes, the bladder of which showed a heavy infection by this myxosporidian, failed to reveal any organisms in the lumina of ureters or uriniferous tubules, lymphoid tissue cells, or blood vessels of the kidneys. In the wall of the ureters of a single host fish examined in fresh condition, a small number of coccidian oocysts of apparently one kind, but in various stages of development, were observed. The mature oocyst contained four spores, each with two sporozoites, which character places the coccidian in the genus Eimeria.

Linton (1901, 1905) showed that the toadfish at Woods Hole, Massachusetts, and Beaufort, North Carolina, were hosts to numerous helminth parasites. The same has been true with the fishes from Maryland and
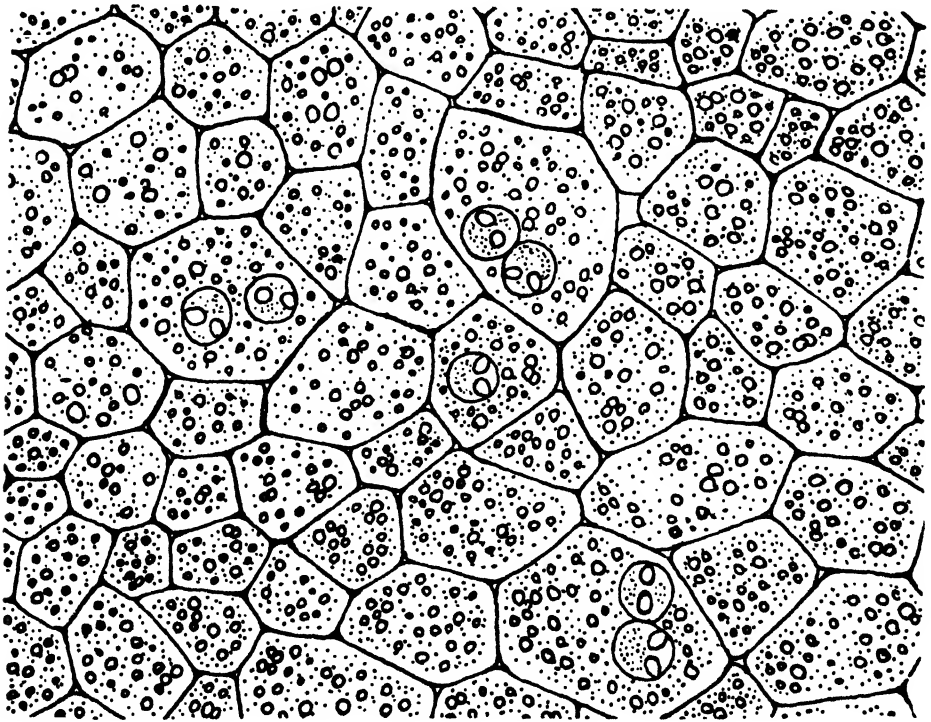
Text Fig. 5.—Surface view of portion of the inner surface of the urinary bladder of a toadfish completely covered by the trophozoites of *Sphaerospora polymorpha.* In life, somewhat flattened. × 1060.

Florida which I have examined during the present study. Every toadfish was infected by several individuals of species of helminths, in tissues and organs associated with the reproductive and urinary systems. Certain of these worms were examined in life, as well as in section preparations, but none harbored either of the two protozoans discussed here.

As to the possible effect of the infection on the host fish, nothing definite can be said at the present moment, since no host fish was entirely free from infection. The behavior and activity of the host fish under laboratory conditions did not indicate the intensity of infection of the bladder by the myxosporidian. Nor were there any external symptoms to show a heavy infection.

Smaller trophozoites appear to be lightly attached to the inner surface of the bladder epithelium, and, therefore, do not seem to affect the cell contents of the tissue cells. As they grow, the attachment becomes firmer, and the trophozoites appear to destroy the cytosome of the host cells, which become increasingly smaller; the trophozoites finally come to lie in the depression of the epithelial cells (fig. 161, center left).

In the bladders studied in serial sections, the thickness of the epithelium or the length of the component epithelial cells varies a great deal. The trophozoites are usually seen attached to the smaller epithelial cells, while the columnar cells adjacent to them do not show any attached organism (fig. 161). It was thought at first that this was due to destruction of columnar epithelial cells by the myxosporidian. However, it was found that this was not the case, for in lightly infected fishes, thin and thick epithelial cells occur without the influence of the parasitic organisms. It may be assumed that the columnar epithelial cells are actively secretional in function, and constantly produce secretions which would make the attachment of trophozoites impossible.

The attached trophozoites grow obviously at the expense of the substances of the host cells to which they are attached, as well as of the liquid and solid substances present in the urine which surrounds them. The epithelial cell nuclei, which are situated near the bases of the cells, do not show any noticeable change as a result of destruction of the outer halves of cells as observed in numerous section preparations treated with Feulgen's nucleal reaction or stained with the nuclear dyes. Thus my observation on the effect of the infection upon the host tissue is in agreement with that of Davis (1917), who stated: "The young trophozoites are attached to the free ends of the epithelial cells (fig. 93) which, however, show no signs of injury. As the trophozoites increase in size they come to lie in depressions formed by the destruction of the ends of epithelial cells (fig. 94). Often the injury to the epithelial cells is carried much further than shown in the figure, in some cases the part of the cell

immediately surrounding the nucleus being all that is left, but even in such cases the nucleus shows little sign of injury."

Generally speaking, unlike histozoic Myxosporidia, coelozoic forms seldom bring about injury to the host organs in which they live. There are, on the other hand, a certain number of authors who observed pathological changes caused by coelozoic myxosporidians on the host organs, such as the gall bladder, urinary bladder, etc. For example, Bauer (1921) reported a cystitis of the bladder of *Esox lucius* infected heavily by *Myxidium lieberkühni*. Even in the most heavily infected bladder no hypertrophy or degeneration of the nuclei of the host epithelium has been noticed in the present myxosporidian. Nor was there any indication that "toxic" stimulation is exercised by the parasite upon the host organ, as was suggested by the same author.

The Trophozoite

In his original diagnosis of the trophozoite of *Sphaerospora polymorpha*, Davis (1917) gave the following description: "Colorless, usually somewhat elongate (fig. 90), but never very irregular in shape; slowly amoeboid. After being on the slide for a short time become rounded and motionless (figs. 86-89). Ectoplasm distinct around younger trophozoites, hyaline, forming one to several large lobate pseudopodia, which in turn extrude several short, conical pseudopodia (fig. 88). In larger trophozoites ectoplasm often not distinguishable except at ends of pseudopodia, which in such cases are composed chiefly of endoplasm. Endoplasm distinctly granular, sometimes vacuolated in smaller trophozoites (fig. 88), but in larger individuals vacuoles are indistinct or absent; small fat globules usually abundant, especially in larger individuals; numbers of rounded sporoblast cells can be distinctly seen."

The majority of the trophozoites are attached more or less firmly to the epithelial cells of the bladder, although many others are suspended freely in the urine. Extremely small trophozoites (fig. 1), measuring less than 10 μ in diameter, are difficult to identify as such in life, except when infected by *Nosema notabilis* (figs. 8, 9), but larger individuals, with their diameters 10 μ or more, can be distinguished without difficulty. As examined in Nemeczek's preparations, the trophozoites that are free in the urine are more or less spherical or rounded (figs. 1-3), or may assume somewhat elongated forms when undergoing change of body form (figs. 4-6). The body form change is, as a rule, carried on very slowly, but in certain individuals is quite rapid. The pseudopodia are ordinarily produced from the comparatively limited area which is in contact with the bladder epithelium, although in some individuals, there may be numerous pseudopodia distributed over the entire body surface (fig. 6). The

pseudopodia are lobose (figs. 2, 3, 12) before they are fully formed, usually broad at the bases and terminating in one or more conical secondary pseudopodia which are sharply attenuated (figs. 4-7), as is the case with numerous coelozoic myxosporidians (Kudo, 1920a).

After being on the slide in the urine of the host fish, the trophozoites become inactive, rounded, and sooner or later degenerate. If the room temperature remains below 20° C., some of them still show noticeable changes of body form after 16 to 20 hours. They appear to retain vitality much longer if they remain in the bladder, even long after the death of the host fish. In one instance, a male toadfish which was dead when it arrived was kept in a refrigerator at about 4° C. for two more days before dissection and examination. More than 50 per cent of trophozoites of various sizes were perfectly normal in appearance, and numerous individuals showed active formation of pseudopodia. Thus, in the case of *Sphaerospora polymorpha,* the trophozoites are able to live in the host organ for at least 50 hours after the death of the host fish, in contrast to the belief sometimes expressed that the active life of a parasitic protozoan ceases with the death of its host.

Trophozoites with a diameter of 10-25 μ are the most abundant in host fishes examined up to the present time (text fig. 5; fig. 162). Larger trophozoites occur less frequently. They are elongated and leaf-like, ellipsoidal, club-shaped, or moniliform in outline. They may reach 100 μ in length, but the body is usually slender. The majority of larger forms are 50-80 μ long by 20-40 μ wide (figs. 15, 16, 161). Davis (1917) wrote that large vegetative trophozoites were about 35 by 50 μ.

The cytoplasm of the trophozoite is colorless and hyaline, and is differentiated into the ectoplasm and endoplasm. The ectoplasm is distinct in the peripheral zone, as well as in the pseudopodia, and does not contain any inclusions. The endoplasm, which makes up the bulk of the body, is variously vacuolated and contains highly refractile granules of variable dimensions, less refractile bodies, granules, small crystals, and other cell inclusions. The appearance of the trophozoites is very similar to other coelozoic myxosporidians I have studied, especially the small trophozoites of *Myxidium lieberkühni* (Kudo, 1921b). The highly refractile spherules, which vary in diameter from about 0.2 to 2.5 μ, dissolve in alcohol, but not in dilute acetic acid or water. Sudan III stains them intensely red (fig. 10). They thus appear to be fat globules.

The less refractile ill-defined bodies, which often contain several minute granules, are stained green against violet-bluish cytoplasm when living trophozoites are treated with acidified methyl-green and are without doubt the trophozoite nuclei. The crystals are regularly rhombic plates and were found in a small number of trophozoites occurring in a few

fish in which they were abundantly present in the epithelial cells of renal tubules of kidney, ureters, and bladder. They may be similar to the haematoidin crystals reported in *Myxidium lieberkühni* (Bütschli, 1881), *Sinuolinea dimorpha* (Davis, 1917), etc. As the central area of the body becomes stained reddish-brown after iodine treatment, there may occur diffused glycogenous substance also. In the trophozoites, which are more or less cylindrical, the part that is in close contact with the epithelial cells appears to be denser and stains more deeply with a cytoplasmic stain than other part of the body, which condition was previously noted by Davis (1917).

The trophozoites are seemingly able to engulf solid particles that are present in the urine. These particles are crystals, spheroidal bodies which are yellowish to brownish and measure up to about 5 μ in diameter (fig. 16), and rounded homogeneous bodies measuring 5-20 μ in diameter (figs. 28, 29). The latter take stains homogeneously and do not reveal any structures which react positively to Feulgen's nucleal reaction (fig. 29). When seen in life, they were looked upon as gemmules that have been observed quite frequently in *Leptotheca ohlmacheri* (Kudo, 1922). Because of their structurelessness and of the presence of similar bodies in the bladder epithelium, I think that these conspicuous homogeneous bodies are excretion products of the bladder epithelium which were engulfed by the trophozoites.

Occasionally the trophozoites are seen ingesting free spores (fig. 13) or other solid material present in the urine. Ingestion of solid particles by myxosporidian trophozoites appears to have first been seen by Bütschli (1881) in *Myxidium lieberkühni,* who wrote: "Man sieht nämlich solche kleinen Formen häufig an losgelösten Epithelzellen der Harnblase derart befestigt, dass ein Theil der Zelle von der Myxosporidie umfasst und eingehüllt wird (fig. 30)." In recent years, Davis (1916) noticed ingestion and digestion of erythrocytes by *Sinuolinea dimorpha* while within the bladder of the host fish.

The trophozoites appear to undergo plasmotomy in the host's bladder, since in a number of individuals observed in life for several hours, plasmotomic division was noted (figs. 17, 18). Under an oil immersion objective, these individuals were found to contain several nuclei. In addition to the simple plasmotomy, multiple division probably occurs also. Larger trophozoites are usually elongated, and the body shows 3 to 5 swellings, between which the cytosome is extremely thin (fig. 15). They represent, most probably, a stage in multiple plasmotomy. Furthermore, the occurrence of enormous numbers of comparatively small trophozoites in the bladders of many host fishes and of closely associated groups of small trophozoites, as frequently seen in fresh preparations (fig. 11), points to multiple

plasmotomic division in the present myxosporidian. On the other hand, there is no indication of gemmation such as has been observed in *Leptotheca ohlmacheri* (Kudo, 1922). Plasmotomy has been observed in a number of coelozoic myxosporidians. Seeing a simple division of the trophozoite of *Chloromyxum leydigi,* Doflein (1898) called the process plasmotomy. This multiplication in *Myxidium lieberkühni* was observed by Cohn (1895), Laveran and Mesnil (1902), Bremer (1922), and others. Laveran and Mesnil observed simple plasmotomy of young trophozoites, while Bremer reported that the trophozoites which he examined multiplied by simple and multiple plasmotomy, in addition to endogenous budding.

Whether the spore germinates in the urine of the bladder in which it has been formed is not definitely known. A spore of *Myxidium lieberkühni* was seen by Bremer (1922) to germinate in the urinary bladder of a dead pike. Judging from the observations on autoinfection by different species of histozoic Myxosporidia (Kudo, 1926), its occurrence in coelozoic forms appears probable. In many smears, as well as section preparations, however, no germinating spores or empty spores have been noticed in the present species up to the present time.

DEVELOPMENT OF TROPHOZOITES AND PROCESS OF SPORE-FORMATION

Although, as was pointed out before, the nuclei of the trophozoite are recognizable in life, the process of division and changes which result in formation of spores could not be followed and studied in life, due to technical difficulties. As in the case of previous investigators of Myxosporidia, my observations are based on fixed and stained smears and sections of naturally infected urinary bladders of many host fish.

The smallest trophozoites observed in smears are shown in figs. 20 to 22. They are spheroidal or ovoid bodies about 5-9 μ in diameter. The cytosome is reticulated and stains light violet or bluish in Giemsa's solution. In the majority of these trophozoites, two nuclei were present, but in some there occurred only a single nucleus. In the latter form (fig. 20), the nucleus is lodged in a small mass of differentiated cytoplasm which stains blue, in contrast to the general cytoplasmic background. It measures about 2 μ in diameter, with peripheral chromatin granules and an endosome which is clearly achromatinic in nature. Compared with the sporoplasm of the mature spore (figs. 89-91, 94, 95), this uninucleate trophozoite differs in size and in having a mass of perinuclear cytoplasm. The difference in size, however, is not so important as the difference in cytoplasmic structure, since the sporoplasm of a large spore is comparable in size (figs. 96, 100), and, moreover, being in a thin portion of the smear, the body appears to be more or less flattened. In all well-studied Myxosporidia, the two sporoplasm nuclei fuse before or after germination from

the spore. The fused sporoplasm nucleus (fig. 90) is much smaller and more compact than that of the uninucleate trophozoite under consideration (fig. 20), and it is lodged in a homogeneous cytoplasmic mass, instead of in a differentiated cytoplasmic mass as in the latter form. Yet this uninucleate condition leads me to maintain that the trophozoite shown in fig. 20 is the youngest stage, which is the closest to the intrasporal sporoplasm.

The binucleate trophozoites shown in figs. 21 and 22 approximate in size the sporoplasm of average spores. There is not much difference in size between them and the sporoplasm which was apparently accidentally extruded from a developing spore by mechanical pressure during the process of preparation (fig. 86). However, the two nuclei in the accidentally extruded sporoplasm are much smaller and characterized by a thick peripheral chromatin zone, and are presumably destined to undergo fusion to produce the single nucleus of the sporoplasm (fig. 90). On the other hand, the two nuclei seen in the binucleate trophozoites (figs. 21, 22) are quite different in structure. One nucleus is similar to that in the uninucleate trophozoite (fig. 20), but the other is imbedded in the general cytoplasm and does not contain any achromatinic endosome. Later changes indicate that the nucleus with an achromatinic endosome and surrounded by a differentiated mass of cytoplasm is the generative nucleus; while the other, without such an endosome, is the vegetative or somatic nucleus.

Nuclear division of the uninucleate trophozoite has not been observed, but it seems probable that the nucleus divides and transforms itself into the two kinds of nuclei found in the binucleate trophozoite, as has been reported in *Sinuolinea dimorpha* (Davis, 1916), *Leptotheca ohlmacheri* (Kudo, 1922), etc.

While in the binucleate state, the trophozoites grow in size, the generative nucleus divides by mitosis (figs. 23, 28), and trophozoites with two generative nuclei and one vegetative nucleus (figs. 24, 25, 31) are formed. The vegetative nucleus has not been seen undergoing mitotic division, and appears to divide amitotically (fig. 26), as in the case of *Leptotheca ohlmacheri* (Kudo, 1922) and of several histozoic Myxosporidia (Davis, 1923; Debaisieux, 1924, 1925; Kudo, 1926). With the growth of body, the size and number of nuclei also increase. There is no definite ratio as to the numbers of the generative and vegetative nuclei. In many individuals (fig. 26), there are two generative and two vegetative nuclei; in some (fig. 27), two generative and four vegetative nuclei; and in still others (fig. 28), four generative nuclei and a single vegetative nucleus. In the sporulating individual shown in figs. 30 and 31, eight generative and five vegetative nuclei and two developing spores were noticeable.

Prior to division the generative nucleus becomes much enlarged, and its chromatin substance, which responds positively by intense coloration

to Feulgen's nucleal reaction, is distributed along the inner surface of the nuclear membrane as a thin but distinct zone. Attached to this zone are chromatin granules which are connected with one another by chromatinic threads (fig. 32). The whole chromatin material then becomes transformed into a spireme (figs. 23, 33). The spireme shortens and breaks up into four chromosomes (figs. 34, 35) which become arranged at equatorial plane (figs. 28, 36-38, 156). At this stage, the chromosomes become short and compact.

The achromatinic fibers make their appearance about the time the chromosomes become distinctive (figs. 34, 35) and appear as delicate parallel fibrils between the two opposite poles (figs. 37-39). These fibrils do not converge at the poles, and no centriole-like granules, as reported by some observers in other species, are seen at any stage. The achromatinic endosome of the nucleus remains often recognizable until the equatorial-plate stage (figs. 23, 37), when it disappears; it reappears after the completion of the division process (fig. 45). In the metaphase, four pairs of chromosomes apparently make up the equatorial plate (fig. 39). The precise mode of division of the individual chromosomes is unknown. In many cases the chromosomes appear to be of different sizes.

During the anaphase, two groups of chromosomes move apart and toward the opposite poles (fig. 40). Not infrequently there are seen very fine chromatinic threads connecting some of the separating pairs of chromosomes. In later stages, the chromosomes become collected near each of the poles (figs. 41-44), and finally two resting nuclei are reconstructed (fig. 45). In the meantime, the differentiated mass of cytoplasm surrounding the dividing nucleus elongates and finally divides into two masses, each containing one daughter nucleus. The spindle fibrils may remain stretched between the two separating nuclei for some time. Judging by the general appearance in smears, as well as in sections, these generative nuclei in specialized cytoplasmic masses are able to move about within the cytosome of the growing trophozoites (figs. 26, 28), appearing in various forms which suggest amoeboid movement.

Certain of the generative nuclei undergo a division which is quite different from that just described. The chromatin material becomes transformed into a spireme (fig. 46) which, however, presently differentiates into two chromatin threads (fig. 47). Toward the extremities of each of these two threads, the chromatin substance becomes condensed (fig. 48). As the nucleus elongates, the two dumbbell-shaped chromosomes become situated in the direction of the elongated nucleus (fig. 49), and each of the two pairs' of chromosomes move apart; the connecting chromatin threads become stretched and finally break off (figs. 50, 51). At the end of the anaphase, the two chromosomes at each pole, which are often of

unequal size, do not undergo synchronous granulation, and consequently there appear more than two chromosomes at one or both poles (fig. 52). When finally the two nuclei are completely reconstructed (figs. 53, 54), the cytoplasmic division follows. The achromatinic endosome, which disappeared earlier (fig. 47), now reappears in one of the daughter nuclei (fig. 54). A similar division figure has often been seen in many species by various observers. Georgévitch (1936) saw stages similar to those indicated in figs. 48-51 in *Myxidium gadi* and interpreted them as phases in mitosis in which four chromosomes unite in two large reniform chromosomes before reaching the poles.

On the basis of the constant presence of one-half the number of chromosomes involved, as compared with normal mitosis, I consider this nuclear division as meiosis, by which the generative nuclei enter their last stage of activity prior to the initiation of spore-formation. Whether there is a second division cannot be stated, but I failed to see any figures suggesting the occurrence of that division.

Various stages in the development of spores have always been traced back to the forms shown in figs. 55-57. Imbedded directly in the cytoplasm (fig. 55), or often in a clear vacuole in the cytoplasm (figs. 56, 57), are two cells in association. Seen in sections, as well as smears, they show irregular outlines, though on the whole spindle-form, and bear a certain relation to the surrounding cytoplasm, as though possessing the capacity of amoeboid movement. Each cell contains a single nucleus, but the two nuclei in association are dissimilar in size and structure. The larger nucleus located in the larger cell shows in almost all cases a large achromatinic endosome (figs. 56, 58), while the smaller nucleus in the smaller cell usually does not contain such an endosome. This association may take place between the two newly divided cells, as shown in fig. 54, instead of between two cells produced by reduction division of different generative nuclei. That the latter is more common, is demonstrated by frequent occurrence of the two associated cells, as shown in figs. 55-57, in which the cells are coming in contact on lateral surfaces.

The two nuclei appear to remain independent and not to fuse with each other, at least during the early part of the period of spore-formation. The associated cells often leave a narrow space between them at the beginning (figs. 56, 58), but they soon become intimately united with each other (figs. 59-62), although the cell boundaries remain distinctly visible for some time. The nuclei divide presently. The division of the smaller nucleus may precede (figs. 57, 59, 62) or follow that of the large one (figs. 64-68), or the division of the two nuclei may be synchronous (figs. 60, 61). The nucleus preparing to divide shows an increase of chromatin substance which becomes transformed into a spireme (figs. 58-

60) that develops into two chromosomes. These chromosomes are most clearly noticeable during anaphase (figs. 59, 62, 64-66). In this mitotic figure, spindle fibrils are difficult to observe. The chromosomes become elongate (fig. 68), but condensed, as they approach the poles, and finally they are broken up into granules in the two daughter nuclei (figs. 63, 69). Thus sporonts with two large and two small nuclei are formed (figs. 69, 70). No achromatinic endosome is visible any more in any of the nuclei. As far as could be determined, the two smaller nuclei do not undergo further division but remain as the sporont (or pansporoblast) nuclei (figs. 78, 80), which may completely disappear when the spore-formation nears completion (fig. 81).

The other two nuclei become much enlarged and filled with chromatin material which is intensely positive to Feulgen's reaction (figs. 70, 71). During division the chromosomes are distinctly visible (figs. 72, 73, 75, 76). As the number of nuclei increases, the chromatin becomes more abundant and appears as heavy threads and coarse granules spread within the nuclei (figs. 74-76). In Feulgen preparations it is noticed that the nuclei are filled with chromatinic reticulum in which chromatin substance appears to be present in diffused state (figs. 77, 78). As the nuclear division continues, there appear in the sporont several compact chromatinic spherules which are occasionally vacuolated in the center, and at the same time the nuclei show a circular area which reacts negatively to Feulgen's reaction. These spherules, which also stain intensely with Heidenhain or Giemsa, have been noted in the developing sporonts of numerous species of Myxosporidia. Erdmann (1917) saw them in *Chloromyxum leydigi* and considered them to be glycogenous bodies; others called them "reduction nuclei." I have observed what I considered extrusion of plasmosomic endosomes at the corresponding developmental stages in the sporont of *Myxosoma catostomi* (Kudo, 1923, 1926). In the present myxosporidian, through the use of Feulgen's nucleal reaction, it has been established beyond doubt that Feulgen-positive substance is abundantly produced during the latter half of the period of development of the sporont and given off to the cytosome in the form of spherules about 0.5-1 μ in diameter. These chromatinic spherules are most frequently found in pairs (figs. 77-79), and in some, two spherules appear to have a connection between them, which suggests that these spherules may break up into smaller bodies by a simple fission. By the time the sporont differentiates into two sporoblasts (figs. 80, 81), these spherules disappear completely in almost all cases. Therefore, I am inclined to think as before (Kudo, 1926) that these chromatinic spherules are used for the formation of the spore-membrane and also of the polar capsules and their polar filaments.

In well-advanced sporonts containing ten or more nuclei, the nuclei become less chromatinic (fig. 79), and when fourteen nuclei are formed

they become definitely grouped in the two developing sporoblasts. Each sporoblast contains two nuclei for the sporoplasm, two for the polar capsules, and two for the valves of the spore membrane. Between the two sporoblasts there are usually visible two degenerating sporont nuclei previously referred to (fig. 80). Of the fourteen nuclei, ten degenerate gradually as the spore-formation proceeds. The four valve nuclei become ovoid, and characterized by a delicate chromatinic ring, while the four capsulogenous nuclei show various sorts of change in form and structure (fig. 80). However, the four sporoplasm nuclei remain normal in appearance and structure: namely, with a thick peripheral chromatin zone with granules and strands (figs. 80, 81). Although incompletely observed, the development of the polar capsules and filaments appears similar to that in *Leptotheca ohlmacheri* (Kudo, 1922). The developing polar capsules often react positively to Feulgen's reaction (figs. 81, 84, 85), showing the chromatinic origin of them, but when completely formed, they do not respond positively (figs. 89, 90). As to the shell-valves, no positive reaction to Feulgen has been noted, in contrast to species such as *Myxidium serotinum* and *M. immersum* (Kudo and Sprague, 1940).

The two sporoblasts continue to develop simultaneously and become transformed into spores. In young spores, the valve and capsulogenous nuclei remain visible for some time (figs. 82-86, 91), the latter persisting much longer than the former (figs. 89, 90). There are two nuclei in the sporoplasm of almost all spores (fig. 89), but in some the autogamous fusion appears to have already taken place (fig. 90). No phases of this union have been observed, but it is probable that a diploid nucleus is formed through karyogamy of two haploid nuclei. The sporont is in almost all cases disporoblastic as described here, but in a small number of cases it appeared to be monosporoblastic. The majority of trophozoites are disporous, and less frequently polysporous. Monosporous trophozoites are relatively rare.

Little was known about the nuclear phenomena at the time Gurley (1893) coined the term "pansporoblast" for "the transparent plasmasphere formed by the condensation of a portion of the plasma around one of the numerous nuclei of the endoplasm of the myxosporidium; in distinction from the sporoblasts which result from the segmentation of the pansporoblast." Mercier (1906) was the first to propose the occurrence of "phénomènes de sexualité" in the life cycle of *Myxobolus pfeifferi.* Since that time, numerous investigators reported autogamous nuclear fusion at some stages of development in various species of Myxosporidia.

Almost all investigators agree that the two sporoplasm nuclei undergo autogamy prior to, or after, the emergence of the sporoplasm as an amoebula. My observations on species of Myxosporidia, including the present form, also agree with this view.

The fact that mitosis occurs in Myxosporidia, became known as early as 1895 when Thélohan published his excellent treatise of these organisms. Mitosis of the trophozoite nuclei is now known in the following species: *Chloromyxum leydigi* (Naville, 1927); *Sphaerospora polymorpha* (Kudo, present study); *Sinuolinea dimorpha* (Davis, 1916); *Myxidium lieber-kühni* (Bremer, 1922a); *Myxidium gadi* (Georgévitch, 1919, 1936); *Zschokkella rovignensis* (Nemeczek, 1922; Georgévitch, 1936); *Sphaero-myxa balbianii* (Naville, 1930); *Sphaeromyxa sabrazesi* (Debaisieux, 1924; Bĕlař, 1926; Naville, 1930; Georgévitch, 1936); *Myxosoma catostomi* (Kudo, 1926); *Thelohanellus swellengrebeli* (Schuurmans Stekhoven, 1919); *Myxobolus pfeifferi* (Mercier, 1908; Keysselitz, 1908; Georgévitch, 1936a); *Myxobolus destruens* (Schuurmans Stekhoven, 1920); *Myxobolus guyénoti* (Naville, 1928), *Henneguya gigantea* (Georgévitch, 1914, 1936). Each of these species has four chromosomes in its generative nuclei, except *Sinuolinea dimorpha,* which has six, according to Davis (1916). Six chromosomes were also claimed for *Sphaeromyxa sabrazesi* by Debaisieux (1924) and Bĕlař (1926), but later works (Naville, 1930; Georgévitch, 1936) show only four.

Concerning the starting point in the spore-formation, there are many views, even in one and the same species. Thélohan (1892, 1895) considered that each set of the two spores of *Myxobolus ellipsoides* and *M. pfeifferi* developed from a uninucleate generative cell which was "une petite sphère de protoplasma à contour net, qui semble limitée par une mince enveloppe résultant de la condensation de sa couche périphérique," and named it "la sphère primitive." Gurley renamed this body, as already stated, "pansporoblast." In this view, the sexual process is carried on in the sporoplasm, where the two nuclei fuse with each other. In recent years, such development was observed in *Sinuolinea dimorpha* (Davis, 1916), *Ceratomyxa coris* (Stempell, 1919), *Leptotheca ohlmacheri* (Kudo, 1922), and *Myxosoma ovalis* (Davis, 1923).

However, by far in a larger number of species of Myxosporidia, the initial stage of spore-formation is brought forward by association of two uni- or bi-nucleated cytoplasmic masses. Naville (1931) gave an excellent discussion of many views presented by various observers on this question. Therefore, I shall omit a general review. The two associating uninucleate generative cells in *Myxobolus pfeifferi* have been called macro- and micro-gametes by Mercier (1909), who believed that there was a complete fusion of both nuclei and cytoplasms. In *Sphaerospora polymorpha,* two uninucleate cells fuse without nuclear fusion, and in this respect the process resembles that found in *Myxobolus toyamai* (Kudo, 1917). The nuclear phenomena in the developing trophozoites of *Sphaerospora poly-morpha* are somewhat similar, as a whole, to those of *Sphaeromyxa*

sabrazesi, S. balbianii, and *Myxidium incurvatum* as reported by Naville (1930), in that there are two types of divisions of the generative nuclei: namely, mitotic, to increase the number of the nuclei, and meiotic, to prepare for the formation of sporonts. However, I have not seen in *Sphaerospora polymorpha* the "4-microgamete stage" reported by Naville in Sphaeromyxa, which appears to have been seen also by Schröder (1907). Nor have I seen in the present species the so-called quartet in which two male and two female gamete nuclei become differentiated as reported by Naville in *Myxidium incurvatum.* In *Myxidium bergense,* Auerbach (1912) observed an association of two similar uninucleate cells to produce a binucleate sporont, somewhat similar to the one described here, but one of the nuclei is said to undergo reduction division before further development of the sporont takes place.

The view of Georgévitch (1923, 1936, 1936a), that the nuclei of the developing sporoblasts of *Myxidium gadi, Zschokkella rovignensis, Sphaeromyxa sabrazesi, Myxobolus pfeifferi,* and *Henneguya gigantea,* are all diploid, and that the two sporoplasm nuclei undergo meiotic division to become haploid prior to autogamous fusion, has not been confirmed by other investigators. Occasionally myxosporidian spores contain four nuclei, but because of their rarity one is led to think that this is an abnormal condition. Such was the case in *Myxosoma catostomi* (Kudo, 1926). In *Sphaeromyxa sabrazesi,* Debaisieux (1924) saw amitosis of the two sporoplasm nuclei, but Naville (1930) did not see a single instance of nuclear division in the sporoplasm. In *Sphaerospora polymorpha,* no spores contained either dividing nuclei or more than two nuclei in the sporoplasm.

THE SPORE

The spore is spheroidal in general form (figs. 93-104). In front view, it is either circular or subcircular, with a slightly flattened anterior margin (figs. 94-96, 100). In end view, it is circular or broadly ovoid and somewhat pointed along the sutural line (figs. 97, 98). In side view, it is oval with a slightly pointed sutural ridge (fig. 99).

The spore membrane is uniformly thick, and composed of two valves which are sometimes asymmetrical. The sutural ridge is distinctly visible in life (figs. 88, 92, 96-104), and coincides with the broadest plane of the spore, so that it cannot be seen in front view (figs. 94, 95). Each of the two polar capsules is, as a rule, connected with the anterolateral margin of the valve close to the sutural plane (figs. 94-96). In many spores the sutural ridge takes unusual or abnormal courses. Most frequently the ridge makes some acute angles with the broadest plane of the spore, so that it can be seen in front view (fig. 87). In a number of spores the sutural ridge is at right angles to the largest axis of the spore, one polar

capsule being located on each side of it (fig. 100). Such spores resemble those of Leptotheca. The surface of the membrane shows, without exception, numerous fine ridges or elevated striae, which give the spore a striated appearance. All striae appear to be uniformly high and thick, unlike those found in certain other myxosporidians, such as *Leptotheca ohlmacheri* (Kudo, 1922), *Myxidium serotinum* (Kudo and Sprague, 1940). There are about 20 to 30 striae on each valve, which are, as a rule, parallel to one another and to the sutural ridge (figs. 87, 92, 96-98, 100, 101). In many spores, however, these striae are not parallel to the sutural line and make various angles with it (figs. 88, 93, 102-104). In still others, there are 2 or 3 ridges which encircle the margin of the valve, and numerous parallel ridges are evenly distributed over the entire valve-surface (fig. 99). Davis (1917) in his description states: "On each side are a number of concentric striations extending around each valve parallel to the sutural line."

There are two polar capsules situated in the anterior half of the spore. They are of nearly the same size, although in a few spores unequal capsules are found. They are pyriform in shape and contain a polar filament which is coiled 3 to 6 times and which is clearly visible in life. The neck of the capsule is drawn out into a fine tube and opens in the shell-valve at the anterolateral margin near the sutural ridge (figs. 91, 92, 94-96). Thus the two polar capsules are extremely divergent in front view. There is one foramen for the capsule on each valve, a condition seen in many other species, as for example, in *Leptotheca ohlmacheri* (Kudo, 1922), *Myxidium immersum* and *M. serotinum* (Kudo and Sprague, 1940).

This divergency of the two capsules is quite uncommon except in the family Myxidiidae. In his original description of the species, Davis (1917) stated: "capsules large, distinctly pyriform. Coiled filaments distinct." In his figs. 88 and 91, Davis showed spores, the two polar capsules of which are nearly parallel to each other, while in those shown in his fig. 89, the two capsules are slightly convergent or parallel to each other. In no one of the spores did Davis figure the divergent capsules. This consistent difference in the position of the polar capsules between Davis' species and my own material puzzled me for some time. Recently, through the kindness of Dr. Davis, I examined two smears of the contents of the bladder of the toadfish that had been prepared by him at the time of his investigation (1917). The smears were fixed with osmium vapor, and stained with Heidenhain's and Delafield's haematoxylin. The Heidenhain preparation showed still distinctly stained polar capsules in developing spores, while mature spores in the smear were too intensely stained to allow any observation. The young or newly matured spores showed in every case

divergent polar capsules, which condition is clearly visible in front view. Therefore, it is held that the normal spore of *Sphaerospora polymorpha* possesses two divergent polar capsules. In this respect, the present species resembles strikingly *Sphaerospora divergens* as observed by Thélohan (1895) and Auerbach (1912).

Occasionally spores with one, three, or four polar capsules (fig. 19) are encountered, which conditions appear to have been brought about by abnormal arrangement of the capsules during the development of disporoblastic sporonts.

The polar filaments are easily extruded from the capsules in fresh spores, when the latter are subjected to mechanical pressure or treated with potassium hydrate or hydrogen peroxide, as I have experienced in my previous studies with various Myxosporidia. When fully extruded, the polar filaments measure 24 to 32 μ in length, and in some cases the tubular nature of the filament could be noticed (fig. 93).

The main mass of the sporoplasm is situated in the posterior half of the spore, but extends anteriorly between the capsules and expands along the anterior margin of the spore (figs. 94-96). The sporoplasm consists of finely granulated cytoplasm, and contains two vesicular nuclei which are usually noticeable in life (fig. 94).

When the spores are fixed and stained, the characteristic feature of a bicapsulated myxosporidian spore becomes plainly visible (figs. 89-91). The valve nuclei may be seen in young spores as delicate rings in Feulgen's preparations (figs. 83-85) or as thickenings in the membrane in Heidenhain or Giemsa preparations. However, they disintegrate much earlier than the capsulogenous nuclei which remain in close association with the developing capsules (figs. 89-91). In some cases the capsulogenous nuclei may remain recognizable even after the two sporoplasm nuclei fuse (fig. 90). The sporoplasm nuclei are almost always two in number and rich in chromatin substance (figs. 84, 85, 89, 91).

The fine striae or ridges present on the outer surface of the spore membrane appear in Giemsa smears to be composed of small granules arranged in linear series at the beginning (figs. 87, 88), but to be continuous fine lines when fully formed (fig. 92).

The fresh spores as viewed in the host's urine or salt solution vary in dimensions. A few small spores measure only 6.5 μ long and wide, and about 5-6 μ thick. The largest spores measure 11 μ in diameter. The majority of the spores however are 7.5-9.5 μ in length and breadth and 7-8 μ in thickness. The polar capsules are 3.8-5 μ long by 2-2.8 μ in diameter. Davis (1917) gave the following dimensions of the spores of *Sphaerospora polymorpha*, which he measured presumably in fresh condition: "diameter of spore 7-10 μ, averaging about 8 μ; capsules 2-2.5 μ by

4-5 μ." As in the case with other species (Kudo, 1921c), fixed and stained spores in permanent smears show smaller dimensions. Spores fixed with Carnoy, Schaudinn, or Bouin, stained with Heidenhain or Giemsa or subjected to Feulgen's reaction, and mounted in Canada balsam or cedar wood oil, average 6.2-8.5 μ long and wide and 5.5-7.5 μ thick, and the polar capsules were 3-4 μ long by 1.5-2.5 μ in diameter.

RÉSUMÉ OF DEVELOPMENT OF *Sphaerospora polymorpha*

The development of the trophozoite and the process of spore-formation in *Sphaerospora polymorpha,* as observed in the urinary bladder of *Opsanus tau* and *O. beta,* will be summarized briefly here (text fig. 6). The youngest stage is a uninucleate trophozoite in which the nucleus is surrounded by a differentiated cytoplasmic mass (1), which gives rise
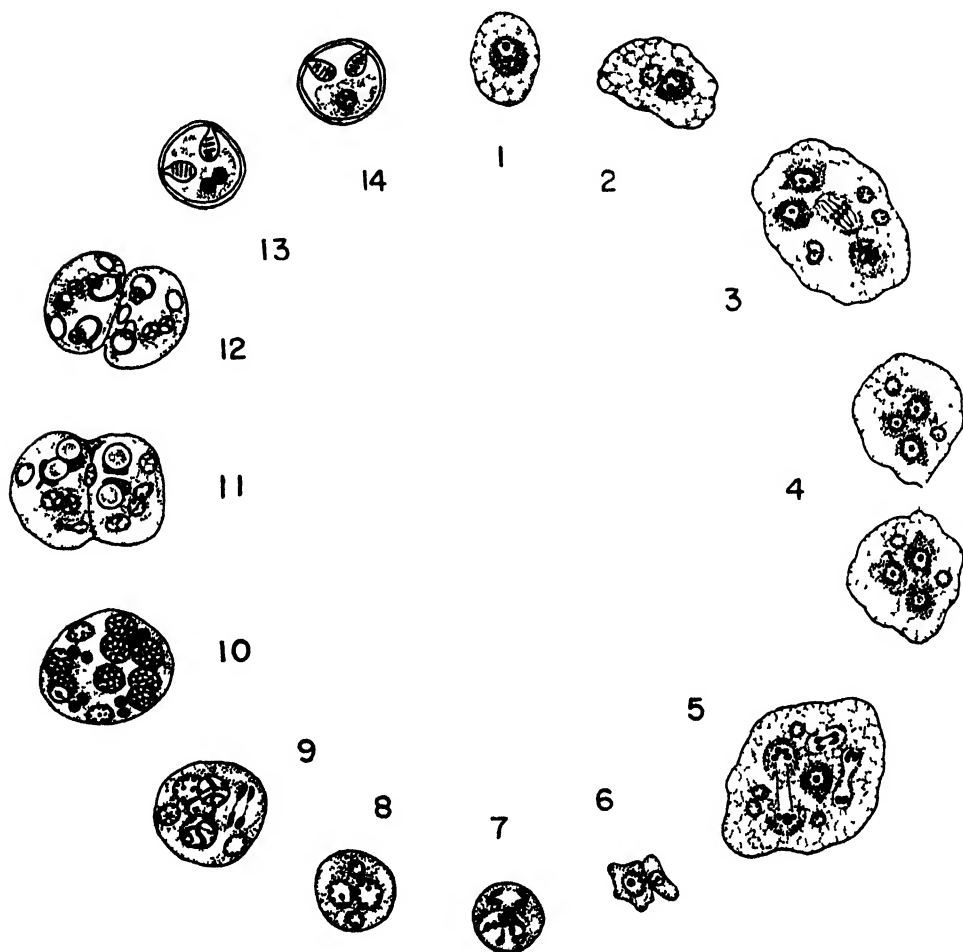
TEXT FIG. 6.—Diagram showing the development of *Sphaerospora polymorpha* in the urinary bladder of the host fish.

to a binucleate trophozoite that contains a generative and a vegetative nucleus (2). The generative nucleus multiplies by mitosis, during which change four chromosomes appear; the vegetative nucleus divides by amitosis (3). Simple plasmotomy increases the number of trophozoites (4); multiple plasmotomy probably occurs also. The generative nuclei undergo reduction division (5) to produce uninucleate generative cells, each with a haploid nucleus, which become associated in pairs to produce a sporont or pansporoblast (6). The cytoplasmic masses fuse, but the two nuclei remain independent, and both undergo division, in which two chromosomes appear (7, 8). The division is repeated (9). The chromatinic substance of the nuclei increases, and small spherules composed of the same substance appear in the cytosome of the developing sporont (10). Finally the sporont becomes differentiated into two sporoblasts, each containing six nuclei (11), and each sporoblast develops into a spore (12). Mature spores first contain two haploid nuclei (13), and then a single diploid nucleus. The gap between 14 and 1 is unknown at present.

Taxonomic Consideration

At the time when Davis (1917) described *Sphaerospora polymorpha*, there were six known species of the genus (Kudo, 1920a). Of these, *Sphaerospora divergens*, which Thélohan (1895) found at Concarneau and Roscoff, France, in the renal tubules of *Blennis pholis* and *Crenilabrus melops*, appears to possess the spore which resembles that of the species under consideration. The spores of *S. divergens* are spherical and measure 10 μ in diameter, sometimes 10 μ by 12 μ. The spore membrane is marked by striae difficult to recognize. The polar capsules are divergent; polar filaments are visible in life, and when extruded under the action of potassium hydrate measure 20-25 μ in length. This myxosporidian was further observed by Parisi (1912) in the kidney of *Crenilabrus pavo*, at Naples, Italy. Auerbach (1912) found it in the urinary bladder of *Hippoglossoides limandoides* in Norway, and showed that the spores were 10 μ in diameter by 8 μ thick. About 4 μ long polar capsules are divergent, and the spore membrane shows a fine striation. In his figures, Auerbach indicated that in front view there are about 20 fine parallel striae in two groups on the shell, and in side view seven and nine parallel striae meet the sutural ridge at acute angles. Jameson (1931) reported this species in the urinary bladder of *Pleuronichthys verticalis* of San Pedro, California, and stated that the spores were slightly smaller than those previously reported from European waters, being 8-10 μ in diameter.

Thus it appears that the spores of these two closely resembling species differ in dimensions. Moreover, the host species are distinctly different, although we do not possess much data as to how much this host-specificity

could be depended upon for taxonomic purposes. I think Davis (1917) was justified in naming *Sphaerospora polymorpha* as a new species.

It may be noted here that since 1917, the following eight species of Sphaerospora have been described: *S. gasterostei* (Schuurmans Stekhoven, 1920), *S. tincae* (Plehn, 1925) (= *S. pernicialis*, Léger, 1929), *S.* sp. (Davis, 1917), *S.* sp. (Southwell and Prashad, 1918), *S.* sp. (Kudo, 1920a), *S. subelegans* (Fantham, 1930), *S. renalis* (Bond, 1938), and *S. notropis* (Fantham, Porter, and Richardson, 1939). None of these species possesses the spore similar to that of the present species.

DIAGNOSIS OF *Sphaerospora polymorpha* DAVIS

Habitat.—In the urinary bladder of *Opsanus tau* and *O. beta*. Beaufort, North Carolina (Davis); Solomons Island, Maryland; Englewood, Florida (Kudo).

Trophozoite.—Amoeboid, with conical pseudopods from limited body surface; usually attached to bladder epithelium, rounded; larger forms elongate. Cytosome differentiated into ecto- and endo-plasms; with numerous fat globules. Simple and multiple plasmotomy. Size up to 100 μ long by 20-65 μ wide; the majority range from 20 to 50 μ in length. Sporont disporoblastic or rarely monosporoblastic. Trophozoite disporous, polysporous, or, rarely, monosporous.

Spore.—Spheroidal; sutural ridge distinct; shell-valves symmetrical, finely striated; striation in many cases parallel, but may be at various angles to sutural line. Polar capsules conspicuously divergent. Fresh spores: 7.5-9.5 μ in diameter, 7-8 μ thick. Polar capsules: 3.8-5 μ long by 2-2.8 μ wide. Fixed, stained, and mounted spores: 6.2-8.5 μ in diameter by 5.5-7.7 μ thick; polar capsules 3-4 μ by 1.5-2.5 μ.

Remarks.—It is extremely common, but does not bring about any noticeable pathological effect on the host fish. The spore of this species resembles closely that of *Sphaerospora divergens*.

MODE OF INFECTION

Although, as was pointed out before, there are numerous species of coelozoic Myxosporidia which inhabit the urinary bladder, ureters, or renal tubules of the kidney of host fish, no experimental evidence is available to indicate how the infection begins. In the case of *Leptotheca ohlmacheri*, which is parasitic in the lumen of the uriniferous tubules of the kidney of frogs and toads, Ohlmacher (1893) wrote: "as to the origin of the myxosporidian infection, we can only conjecture that it must have occurred by way of the cloaca to the bladder, eventually lodging in the kidneys." I have already pointed out that this view is untenable "because

myxosporidian spores have no power of locomotion and have never been seen or been made to germinate in water outside of the host" (Kudo, 1922). Experimental germination of the spores in the pylorus or duodenum of the frog suggested that the liberated amoebulae probably penetrate through the wall of the digestive tract, appear in the coelomic fluid, and finally reach the uriniferous tubules.

Regarding *Sinuolinea dimorpha,* parasitic in the urinary bladder and Wolffian ducts of *Cynoscion regalis,* Davis (1916) observed that "spores when placed on the slide without previous exposure to sea water, and mixed with a drop of fluid from the pyloric caeca of the host, usually germinated within five to fifteen minutes," and suggested that "it appears probable, therefore, that the free spores, when taken into the intestine of the host, germinate, and the sporozoites, as free amoebulae, actively make their way into the urinary bladder."

In the toadfish, the digestive canal and urinary organ are not directly connected at any point, and there is no possibility of the amoebulae which become free in the intestine leaving the anal opening and entering the urinary bladder. It is therefore suggested that the amoebulae emerge from the spores in the intestine, penetrate through the gut wall, and enter the coelom, finally reaching the urinary bladder. Exact information as to how this myxosporidian reaches the bladder remains to be obtained through experimental infection in the future.

V. *NOSEMA NOTABILIS* KUDO

OCCURRENCE

IN ORDER TO ascertain whether the host fish tissues were infected by the microsporidian, serial sections of the kidneys, ureters, and gonads of eleven fish were carefully examined. The urinary bladders of these fishes not only harbored large numbers of the trophozoites of *Sphaerospora polymorpha* in which *Nosema notabilis* was abundantly present, but also contained many spores of this microsporidian floating freely in the urine. Up to the present time, however, this microsporidian has not been observed in any of the host tissue cells. In all fishes examined, many helminths were found in various viscera. Since several helminths are known to be hosts for microsporidians (Kudo, 1924b), it was natural to suppose that there might be some individuals of these worms which were infected by *Nosema notabilis.* Although many worms taken from viscera in close association with the urinary system of the host fish were examined in smears and sections, none showed any infection. Therefore, I am led to hold that *Nosema notabilis* is a specific and exclusive parasite of the myxosporidian *Sphaerospora polymorpha.*

The Sphaerospora trophozoites present in all host fishes examined, were infected in turn by *Nosema notabilis* to a varying extent. When the infection was intense, isolated spores could easily be detected in the urine of the fish bladder in an ordinary fresh smear (fig. 160). In cases of slight infection, there were few free spores, and it was necessary to search several microscopic fields before finding one. In one of the heaviest infections, it was estimated roughly that more than 75 per cent of the myxosporidian trophozoites present in the bladder were infected by *Nosema notabilis* (figs. 163, 164, 175), and in the lightest infection, less than one per cent of the myxosporidian trophozoites appeared to be infected. Because of the strong refractility, the mature spores of the microsporidian are easily recognized in life under a comparatively low magnification. On the other hand, the detection of schizogonic as well as sporogonic stages in life can only be made out with an oil immersion objective and proper illumination.

Host trophozoites of various dimensions are all infected by the microsporidian. However, trophozoites which are 50 μ or more in length are seldom seen heavily infected, and those which are less than 40 μ in diameter are most frequently heavily loaded with the microsporidians (figs. 8, 147-158, 163, 164, 173-175). In the heavily infected host trophozoites, the host nuclei appear to have degenerated (figs. 154, 158, 173) or hypertrophied (figs. 150, 151), and there is a complete inhibition of sporulation processes. These changes would most probably result in the total degeneration and disintegration (fig. 174) of the host bodies, which then would set free the microsporidian spores in the urine. Perhaps this accounts for the absence of heavily infected large trophozoites, as the infection brings about degeneration before the hosts are able to grow into larger trophozoites. Undoubtedly, the microsporidian can be considered as pathogenic to the host myxosporidian.

It is occasionally difficult to determine in life whether the Nosema spores present in a small host trophozoite developed in, or were ingested by, the latter, especially when only a few spores are involved. The four spores of *Nosema notabilis* shown in fig. 9 appeared fully normal in appearance, and therefore are considered to have developed within this host trophozoite. More or less heavily infected host trophozoites are usually without pseudopodia and are invariably rounded (figs. 8, 9), although uninfected individuals present in the same field show distinct pseudopodia (figs. 1-7).

Léger and Duboscq (1909) discovered *Nosema frenzelinae*—the very first authentic record of microsporidian infection in a protozoan—in *Frenzelina conformis*, a cephaline gregarine, parasitic in the intestine of *Pachygrapsus marmoratus* at Cavaliere, France. This microsporidian was found in the cysts as well as sporadins of all ages of this gregarine.

Ordinarily, almost all the gregarines present in a crab were infected, although not all crabs harbored infected host protozoans, and the host crab tissues were free from infection. The infected gregarines grew and encysted in pairs; the nuclei underwent division, but gametogony did not take place, which the two authors referred to as a phenomenon of parasitic castration in a protozoan.

The same authors (1909a) further noticed another microsporidian, *Perezia lankesteriae*, in an acephaline gregarine, *Lankesteria ascidiae*, occurring in the intestine of *Ciona intestinalis* at Cette, France. In this case also, the microsporidian was exclusively gregarinophilous and did not invade the Ciona tissues. Moreover, only adult cephalins or sporadins which were extracellular were infected, all intracellular forms being free from the microsporidian.

In the case of *Nosema marionis* (Thélohan) which, according to Stempell (1919), is an exclusive parasite of the myxosporidian *Ceratomyxa coris* Georgévitch (1916), inhabiting the gall bladder of *Coris julis* and *C. giofredi* in coastal waters of France, Georgévitch (1917), who held that the two cnidosporidians were co-existing in the amoeboid individuals "par la plasmogamie accidentelle des plasmodies de ces deux parasites," remarked that in a large proportion of the two parasites both organisms underwent sporulation, which suggests that the microsporidian infection in the Ceratomyxa trophozoites was quite common and harmless. Stempell (1919) who found that the association of the two cnidosporidians was in reality one of parasitism, states that *Nosema marionis* is a common parasite of *Ceratomyxa coris*. Stempell studied the two host species of Coris and found that of 36 Ceratomyxa-infected fish, 15 contained trophozoites of *Ceratomyxa coris* that were infected at least in part by *Nosema marionis*. As to the effect of infection on the host Ceratomyxa, Stempell observed that since the spore-formation of *Ceratomyxa coris* was not affected by *Nosema marionis*, even when the infection was heavy, the microsporidian did not seem to harm the host myxosporidian to any noticeable extent. Thus it appears that *Nosema notabilis* is the sole true pathogenic microsporidian parasite in protozoa.

Schizogony and Sporogony

The earliest development stage of *Nosema notabilis* has been found in small host trophozoites. It was a minute binucleate body which measured 0.5-2 μ in diameter. The irregular outline of its body indicates that it probably is able to undergo amoeboid movement (fig. 116). It resembles very closely the sporoplasm of the spores which have extruded the polar filaments under experimental conditions (figs. 114, 115). This binucleate schizont divides by a binary fission into two uninucleate schizonts (figs. 116-120, 155-157). Obviously division is repeated (figs. 121-127, 150).

When the host trophozoites multiply by plasmotomy, the daughter tropho-
zoites remain infected by the microsporidian.

The nuclei, which respond positively to Feulgen's nucleal reaction, are
compact granules without any recognizable internal differentiation. The
nuclear division is seemingly amitotic, as observed in various species of
Nosema in the past. When the uninucleate schizonts enter the second
phase of development, the body becomes enlarged, and assumes a spindle-
form with first short (figs. 128, 129) and later much drawn-out ends
(figs. 130-133). As the body grows, the conspicuous, compact nucleus also
enlarges itself and undergoes an amitotic division which proceeds slowly,
so that various phases are quite frequently observed (figs. 129-131, 151,
152). The individual nuclei are compact and often appear more or less
triangular in shape, with the bases facing each other. The clear zone
which was present around the parent nucleus becomes enlarged and elon-
gates as the nuclear division progresses, which indicates an increase in the
amount of nucleoplasm at this stage. In highly flattened smears, the
nucleus of the schizont is often greatly spread out (fig. 134) and shows
7 to 10 minute chromatin granules with connecting threads, but its di-
vision is clearly amitotic (figs. 135, 136, 152).

In *Nosema marionis*, Stempell saw a direct nuclear division which he
stated could be called a primitive karyokinesis, since he noticed the ends
of the dividing nucleus were characteristically pointed, and in what he
designated as an anaphase there was a "wurstförmige Verdickung" be-
tween the division plane and each of the poles. Similar appearances were
noticed in *Nosema notabilis* (fig. 151), but I find no ground to maintain
that the division is indirect. The spindle-form schizonts have previously
been seen in numerous species of Microsporidia, such as *Nosema bom-
bycis* (Stempell, 1909; Kudo, 1916; Foà, 1924), *Stempellia magna*
(Kudo, 1925a), *Nosema marionis* (Stempell, 1919), *Thelohania legeri*
(Kudo, 1924), *Nosema nonagriae* (Schwarz, 1929), and *Thelohania
ephestiae* (Mattes, 1928). In *Nosema binucleatum*, Weissenberg (1926)
observed these forms in abundance. He considered the individuals
("Schlauchzellen") such as shown here in figs. 134-136 and 153 degener-
ating forms. I am inclined to think that they are extremely spread-out
normal schizonts rather than degenerating individuals.

The two nuclei of spindle cells move towards the opposite extremities
which continue to grow out (figs. 130, 131), and the central portion be-
comes constricted (figs. 132, 133). In the meantime, each nucleus under-
goes a division once more (figs. 137, 138). The two schizonts may now
separate or remain together (figs. 139, 141), and in a comparatively small
number of cases, each of these daughter schizonts may divide again, or
the two nuclei in one daughter schizont may move apart and undergo
similar changes, resulting in the formation of three binucleate pyriform

schizonts, which remain in a chain (fig. 140). This chain formation has been reported previously in several species of Microsporidia.

Finally, binucleate sporonts (figs. 143, 144) are formed, which transform themselves directly into sporoblasts, and in turn into the spores. The number of nuclei remains two throughout these changes. The cytoplasm draws away first from one end (fig. 145) and then from the other, thus forming the girdle-shaped sporoplasm (fig. 146). How the remarkably long polar filament becomes developed in a comparatively short time is entirely unknown in the present species.

In all Microsporidia in which the process of spore formation has been observed, the sporoblast is either uni- or bi-nucleate. A number of workers, as Mercier, Stempell, Léger and Hesse, etc. (Kudo, 1924a), had been inclined to think that during the development of a sporoblast into a spore, there occur further divisions or breaking up of the nuclei, some remaining in the sporoplasm, others controlling the formation of the spore membrane and polar filament. For example, Stempell (1919) maintained that the development of the spore of *Nosema marionis* was similar to that of *N. bombycis* (Stempell, 1909), and concluded as follows: "Es scheint, als ob auch hier schliesslich sieben Kerne, d.h. vier Amoeboidkeimkerne, zwei Schalenkerne und ein Polkapselkern entstehen." His figures showing this so-called nuclear division, appear to be simple binucleate sporoblasts or young spores as seen in *N. notabilis*. Stempell's fig. 64 especially, which is supposed to illustrate the 7-nucleate sporoblast, is far from convincing. Fantham (1939) still holds the view which he expressed in his study of *N. apis* that the single nucleus in the sporoblast of *N. cactoblastis* and *N. cactorum* divides into five nuclei (two for the membrane, two for the sporoplasm, and one for the polar capsule and filament). Here, also, there is insufficient evidence to support the view. These changes are similar to the process of spore-formation clearly observable in all Myxosporidia, but there is no evidence to justify such a comparison. In *Thelohania legeri* and *T. indica* (Kudo, 1929), the nucleus of the sporoblast divides in two, and one part seems to be concerned with the formation of the polar filament, while the other remains as the sporoplasm nucleus. In *Stempellia magna* (Kudo, 1925a), an unusually large spore-producing microsporidian, and *Nosema aedis* (Kudo, 1930), the sporoplasm contains a single nucleus. In *Stempellia magna*, with the condensation of the sporoblast cytoplasm towards one end, and appearance of a large clear space towards the other, there appear granules which stain less intensely than chromatin material and which apparently become transformed into the polar filament (Kudo, 1925a). In his studies of various Microsporidia by means of Feulgen's nucleal reaction, Jírovec (1936a) did not observe any division of the nuclei of the sporoblast. Trappmann (1923, 1926) noticed in Giemsa-stained preparations of *Nosema apis* that the two nuclei of a sporoblast

segment off parts which wander into the posterior vacuole in granule form and join with fine cytoplasmic strands to produce the polar filament. With Feulgen's reaction, Jírovec showed that during this change in *N. apis*, the sporoblast as well as the spore were binucleate, and there was no visible nuclear participation in the formation of either spore membrane or polar filament.

During the spore-formation of *Sphaerospora polymorpha* (p. 25) and numerous other Myxosporidia, each polar capsule originates within a special uninucleate capsulogenous cell, and the filament is formed under the control of the nucleus (Kudo, 1922). Upon complete development of the capsule and its filament, the nucleus may still remain as such, though it finally degenerates completely. The polar filament of Myxosporidian spores is comparatively short, though much larger in diameter. The polar filament of *Nosema notabilis* and other microsporidians is relatively much longer and very much finer than that of a myxosporidian. One may suppose, therefore, that it develops during the maturing of the spore, under the control of a special nucleus. In fact, several observers have reported such a nucleus, but it has not been seen in cases where the developing sporoblasts were subjected to Feulgen's nucleal reaction.

In the sporoblasts of *Nosema notabilis*, I have examined numerous individuals which were subjected to Feulgen's nucleal reaction or were stained with Giemsa's solution or Heidenhain's haematoxylin, but I have failed to find any nuclear structure in addition to the two nuclei of the sporoplasm. Since the two nuclei are quite dissimilar in size and form, one may assume that one controls the formation of the membrane and the filament, while the other remains as the generative nucleus.

The early phases of the development of Microsporidia have not been seen in many species. In a few instances of experimental infection, certain portions of the development have been seen, but in no case has observation in life been carried through. In *Stempellia magna*, the spores are large, and I was able to observe part of the early developmental phase in life (Kudo, 1925a). The uninucleate sporoplasms emerge from the spores as amoebulae and apparently penetrate through the gut epithelium of the host *Culex* larva, although the actual penetration was not seen. In the case of *Nosema bombycis*, Stempell (1909) maintained that the emerged binucleate amoebulae become uninucleate bodies by fusion of the two nuclei. He coined the term "planonts" for these 0.5-1.5 μ large bodies which were said to multiply rapidly: "Sehr häufig liegen die jungen Planonten auch noch in der Nähe leerer Sporenhüllen, sind aber meist bereits in lebhafter Vermehrung durch Zweiteilung und Knospung begriffen, so dass man gewöhnlich ganze Nester antrifft." Stempell thus maintained that the planonts undergo divisions in the fore- and mid-gut lumen one or two days after ingestion of spores and also in the "bloodstream" of *Arctia caja*.

With respect to *N. marionis,* Stempell (1919) states that its development is similar "im wesentlichen nach dem Schema" for that of *N. bombycis.* In this case, Stempell observed all stages in the cytosome of host trophozoites and added no further information except that the earliest stage was a uninucleate planont. No students of Microsporidia have been able to confirm Stempell's view that the two nuclei in the amoebula fused into one before beginning development. However, a number of workers reported the same changes in other species of Microsporidia, which were entirely based upon stained smears and sections. For example, Trappmann (1926) by studying stained smears of *N. apis,* makes the following statement:

Der aus der Spore ausgeschlüpfte Planont ist amöboid beweglich und zeigt deutlich zwei Kerne. Durch Verschmelzen der beiden Kerne (Autogamie) treten bald einkernige Planonten auf, die bei Neuinfektionen in Ausstrichpräparaten wiederholt gefunden wurden. Schon im Planontenstadium ist der Parasit in der Lage, sich durch successive Zweiteilung stark zu vermehren und grössere Kolonien hunger Planonten zu bilden, die Man auf Schnitten in den Falten des Mitteldarmes finden kann. Die Planonten wandern zu den Epithelzellen des Mitteldarmes hin und dringen durch den Stäbchensaum in diese Zellen ein.

Stempell's original idea seems to be based on an analogy with the early development of myxosporidian spores, in which autogamous union of the two nuclei of the sporoplasm takes place. Trappmann seems to have simply followed this idea without showing concrete evidences for so doing. The majority of recent workers engaged in solution of this phase of microsporidian development are uncertain about the nuclear change at this stage, since living organisms cannot continuously be observed. In connection with the early development of *Plistophora blochmanni,* Zwölfer (1926) makes the following statement:

Es war anzunehmen, dass die Amöboidkeime diese leeren Hüllen bereits verlassen hatten und im Darmlumen frei auftraten. In der Tat konnte das Vorhandensein einer grösseren Anzahl von kleinen, rundlichen bis ovalen im ganzen etwas unregelmässigen Gebilden im Darm festgestellt werden. Sie lagen teils dicht neben leeren Sporenhüllen, teils in einem geringen Abstand von solchen (Taf. 13, Fig. 33). Nach Grösse und Aussehen stimmten diese Körper völlig mit jenen Amöboidkeimen überein, die kurz vor dem Verlassen der Sporenhülle standen. Ich deute sie daher als ausgeschlüpfte freie Amöboidkeime. Diese Gebilde waren ein- oder zwei-kernig. Im ganzen überwogen die zweikernigen Formen. Bei einigen zeigte die chromatische Substanz einen mehr aufgelockerten, bei anderen wiederum einen mehr kompakten an die Verhältnisse im ruhenden Sporenkeim erinnernden Bau. Irgendwelche Anhaltspunkte, dass eine Verschmelzung der beiden Kerne stattfindet, dass somit die freien einkernigen Amöboide aus den entsprechenden zweikernigen hervorgehen, habe ich nicht gewonnen. Auch habe ich keinerlei Beobachtungen gemacht, dass die zweikernigen freien Amöboide einer Teilung ihres Protoplasmakörpers durchmachen.

Schwarz (1929), who also made a careful study of *Nosema nonagriae,* states:

Der Amöboidkeim der Spore behält anschneinend nach dem Ausschlüpfen seine beiden Kerne bei (Stadium 1). Bevor nun die vegetative Vermehrung durch Schizo-

gonie eintritt, glaube ich das einkernige Stadium (2) annehmen zu können. Jedoch fehlt mir dafür ein exakter Beweis. Die beiden Kerne des Amöboidkeimes würden nach dieser Annahme also zu einem verschmelzen.

In *Nosema binucleatum,* Weissenberg (1926) saw no nuclear fusion in the binucleated amoebula, and Mattes (1928) believed that the emerged binucleate amoebulae of *Thelohania ephestiae,* found among empty spores in the haemocoele or in newly infected fat bodies of the host, remained binucleate.

In my study of *Nosema bombycis* (Kudo, 1916), I did not find the planont stages described and figured by Stempell, in which a uninucleated round body increases rapidly in number by division. Foà (1924), also working on the same microsporidian, did not find living individuals in this stage, since she wrote:

Non mi è stato possibile vedere in nessun caso nè in strisci di emolinfa, nè in sezioni di bachi, quella divisione dei planonti che nessuno, dopo Stempell, ha riscontrato. Mi sembra che le figure relative di Stempell (125-126-127) siano troppo poco dimostrative; si aggiunga che sono tolte dall'*Arctia caja* e non dal baco da seta. Ritengo che il planonte diventi subito intracellulare cioè si transformi in meronte, senza dividersi prima, e che appena fissato o poco prima di fissarsi diventi uninucleato per la fusione dei due nuclei.

However, no students of Microsporidia doubt the presence of extracellular stages between the emerged amoebulae and intracellular schizonts. Trager (1937) apparently carelessly misinterpreted the planonts as merely extracellular forms, instead of the original meaning of the term as coined by Stempell. The fact that his silkworm tissue culture contained "wandering cells full of parasites" indicates simply that there is an extracellular stage of the organism following the emergence from the spore, as has been believed by all, and there is no evidence at all to show that actively multiplying planonts of Stempell were present in the haemocoele. Therefore, the following statement made by Trager is clearly incorrect: "The one successful case proves unequivocally the presence, in the blood of silkworms which have recently ingested spores, of minute extracellular infective forms, the 'planonts' of Stempell, the proof for the existence of which has been doubted (Kudo) and has heretofore rested solely on morphological evidence."

THE SPORE

The mature spores are ovoid to ellipsoid, with unequally rounded extremities (figs. 105, 160). When a mature spore is examined in life, it may be composed of a homogeneous protoplasm which fills the spore cavity (figs. 105, 160), or when focused through the axis, it may show a clear space at the more rounded end (figs. 106, 107). Though ordinarily called a vacuole, it invariably shows a minute granule, and in certain spores, a filamentous structure spreading from side to side is also notice-

able. Quite frequently, nearly mature spores appear pyriform, with a comparatively large clear space near the broader extremity (fig. 107). In such a spore, several transverse striae may be found in the remaining portion of the cavity.

The spores vary more or less in size. The average fresh spores measure 3.3 μ long by 2 μ in diameter; but the length varies from 2.9 to 4.8 μ, and the width, from 1.4 to 2.5 μ. The smallest spores measured 2.9 μ by 1.4 μ, and the largest, 4.8 μ by 2.5 μ. Extreme diversities in size and form of the spores of the same species of Microsporidia are not uncommon; for example, the spores of *Nosema marionis* were reported by Stempell (1919) as varying from 1.5 to 7 μ in length, while Thélohan recorded 8 μ as their length.

As in the great majority of Microsporidia, the internal structure cannot be made out in fresh spores, so that it is necessary to resort to fixation and staining. The spore membrane of *Nosema notabilis* is of uniform thickness and composed of a single piece, as found in the majority of microsporidians.

When the spores are fixed with Schaudinn's or Bouin's fluid and stained with Heidenhain's iron haematoxylin, a band-shaped ring of variable width and form becomes deeply stained in the middle of them (fig. 108). Slightly to one side of the anterior tip, there is invariably seen a compact granule from which extends towards the band a delicate less deeply stained filament. This granule, that is apparently the basal thickening of the polar filament, has been seen in the spores of numerous species. It has been noticed in *Nosema bombycis* (Stempell, 1909; Kudo, 1916), *Plistophora macrospora* (Léger and Hesse, 1916), *Plistophora simulii* (Debaisieux and Gastaldi, 1919; Debaisieux, 1928), *Glugea anomala* (Debaisieux, 1920), *Thelohania legeri* (Kudo, 1921a), *Stempellia magna* (Kudo, 1925a), *Plistophora blochmanni* (Zwölfer, 1926; "Polkörper"), *Thelohania ephestiae* (Mattes, 1928), *Nosema nonagriae* (Schwarz, 1929), *Perezia legeri* and *P. mesnili* (Paillot, 1929).

Posterior to the band is an area which is still less deeply stained and is delimited by a filamentous border (fig. 108). When the preparations are further decolorized, the less deeply stained portions noted above become completely destained and unrecognizable, and the band-ring is now seen stained lightly, revealing two compact short rod-shaped nuclei which are deeply stained (fig. 109). Such a spore if seen endwise shows clearly that the band-form protoplasm is a ring with two nuclei imbedded in the periphery (fig. 110).

When the spores are stained with Giemsa's solution, the band-ring of varying width, containing two compact nuclei, becomes conspicuously noticeable, while the parts between this band and the two extremities remain unstained as "vacuoles" of various shapes (figs. 113, 152, 158).

In some spores, the filamentous structure extending between the band and a point near the anterior tip could be noticed (fig. 113, right). The nuclei, which are often of unequal form and size, are placed side by side so closely that it is often difficult to distinguish them.

When the spores are fixed with Schaudinn's, Carnoy's or sublimate-acetic mixture and subjected to Feulgen's nucleal reaction, two closely associated nuclei become distinctly visible near the middle of the spore, although other structures are hardly noticeable (figs. 111, 112). From these observations, it is considered that the binucleate sporoplasm is a girdle located near the middle of the spore.

When the spores are subjected to mechanical pressure or treated with hydrogen peroxide, the polar filament is extruded from the narrower anterior end (figs. 115, 116, 165-170). The process of extrusion is similar to that observed before in other species (Kudo, 1913, 1918, 1925a). Fully extruded filaments measure 45 to 62 μ in length. Frequently the filaments show some 15 to 20 undulations of nearly the same height, but soon they become straightened, though the distal portion may exhibit some 8 to 10 undulations, as was observed in *Nosema apis* (Kudo, 1921). Incompletely extruded filaments usually show a small knob at the distal end, as previously observed in many species (Kudo, 1925a).

As to the function of the polar filament of the microsporidian spore, I have summarized before the information available up to 1924 (Kudo, 1924a). The only additional paper which has appeared since that time is that of Ohshima (1937) on *Nosema bombycis*. Ohshima maintains that the binucleate sporoplasm leaves the spore through the extruded filament and "is directly injected by the filament into the tissue." This author failed to take into account the fact that the filament when extruded measures 57-72 μ in length (Kudo, 1913) and that it is an extremely fine structure, with an estimated diameter of 0.1 μ. Stages indicating the supposed passage of the sporoplasm as amoebula through this "tubular filament" are not described, nor does Ohshima consider the force with which the amoebula is "injected" through the filament without injury. On the other hand, actual emergence of the amoebula from the foramen of the spore has been observed in a number of species by different investigators; for example, *Nosema apis* (Trappmann, 1923, 1926), *Stempellia magna* (Kudo, 1924a, 1925a), *Plistophora blochmanni* (Zwölfer, 1926). Therefore, the hypothesis of Ohshima does not seem to hold true.

The characteristically resistant membrane of the microsporidian spore has been found to be of a single piece in the majority of known species. Several investigators claim to have seen two valve-cell nuclei in the developing sporoblasts. In *Nosema bombycis*, Stempell (1909) described two such nuclei which other workers who studied the same species did not observe. Fantham and Porter (1912) figure similar nuclei in *Nosema*

apis. In *Pyrotheca incurvata* and *Cougourdella magna,* Hesse (1935) figures two "parietal nuclei," although the spore membrane of the mature spores is a single piece. In certain species, the spore possesses a distinctly visible longitudinal line, which appears to be the sutural line of two valves of the membrane. In *Thelohania opacita,* I have observed splitting of the two valves along this line (Kudo, 1924a, 1925). In *Glugea anomala, Thelohania giardi* (Thélohan, 1895), *Plistophora simulii* (Lutz and Splendore, 1904) and *Plistophora* sp. (Mercier, 1908), a sutural line was noticed on the spores.

From the observations described above, it is concluded that the spore of *Nosema notabilis* is composed of a single-piece membrane, the binucleate sporoplasm is a girdle-shaped ring, and the spirally-coiled polar filament is located in the space unoccupied by the sporoplasm. Whether the polar filament is enclosed within a polar capsule, as in the case of *N. bombycis* (Kudo, 1916), cannot be determined.

With respect to the structure of the microsporidian spore, there have appeared a large number of papers. Some of the differences in interpretation are due to the minuteness of the object and the technical difficulties in demonstrating the inner structure. Furthermore, there has been a tendency among many authors to generalize specific information on one or a few species over the entire group of Microsporidia. Since my previous summaries on the structure of microsporidian spores (Kudo, 1920, 1924a, 1930, 1930a), very little knowledge has been added, nor does the present study contribute much to the information on this subject. The question will undoubtedly continue to be discussed so long as the present limitation in optical apparatus exists.

Based on observations on many species of Microsporidia belonging to different genera, I maintain the previously expressed view that "structural variations exist among the spores of different species." These variations may be conveniently grouped under the following types:

(1) The spore is ovoidal and contains two polar capsules, one at each end of the spore. The sporoplasm is located between the polar capsules. Thus it is comparable with various Myxosporidia in the family Myxidiidae (Kudo, 1920a). The sole species of this type, *Telomyxa glugeiformis,* has been seen only by Léger and Hesse (1910) in the adipose tissue of the larvae of *Ephemera vulgata* in France.

(2) The spore is cylindrical, with or without a caudal prolongation. Polar filament is composed of rod-like portion and a filament. According to Léger and Hesse (1916), the sporoplasm is located at the posterior end of the spore, but according to Jírovec (1936, 1936a), the sporoplasm, with one or two elongate nuclei, surrounds the rod, and is not at the posterior end. Examples: *Mrazekia caudata* (Léger and Hesse, 1916), *Bacillidium argoisi* (Léger and Hesse, 1916; Jírovec, 1936).

(3) The spore is pyriform. The polar capsule is conspicuous and median or lateral in its position, occupying the anterior two-thirds or nearly the entire length of the spore. The sporoplasm is located in the posterior region of the spore cavity, but may extend toward the middle. Examples: *Plistophora macrospora* (Léger and Hesse, 1916), *Stempellia magna* (Kudo, 1921a, 1925a), *Glugea danilewskyi* (Guyénot and Naville, 1922), *Pyrotheca incurvata* (Hesse, 1935). In *Nosema aedis*, I have noticed, in addition to the typical spore, various spores in which the sporoplasm was not terminal, but located near the middle as a complete or broken ring (Kudo, 1930).

(4) The spore is ovoidal or ellipsoidal. The sporoplasm is a girdle-like ring, located near the middle, surrounding the spirally coiled polar filament. The polar capsule may or may not be present. The great majority of the known Microsporidia possess spores which come under this group. The present microsporidian is an example. Some others in which the polar capsule was reported to be present are *Nosema bombycis* (Stempell, 1909; Kudo, 1916), *Thelohania giardi* (Mercier, 1909), and *Nosema nonagriae* (Schwarz, 1929). Those without the polar capsule are *Plistophora longifilis* (Schuberg, 1910), *Glugea anomala, G. hertwigi* (Weissenberg, 1913), *Plistophora blochmanni* (Zwölfer, 1926), and *P. simulii* (Debaisieux, 1928).

Common to all microsporidian spores is the polar filament. It has been seen coiled within the immature spores of several species, as for example, *Stempellia magna, Nosema aedis,* etc., and has, as far as my observation goes, been demonstrated to extrude under experimental conditions. Indeed, the polar filament is the most important characteristic for the identification of the microsporidian spores.

As was pointed out above, the sporoplasm varies in its position from median to terminal, and in form, from a complete or incomplete ring to a spheroidal mass. As to the number of nuclei present in the sporoplasm of the spore, there are diverse observations. The tetranucleate condition of the sporoplasm first reported by Stempell (1904, 1909, 1919) in *Glugea anomala, Nosema bombycis,* and *N. marionis,* and by Mercier (1908) in *Thelohania giardi,* has not been observed by recent workers. And in the case of *Nosema bombycis,* all other investigators found only one or two nuclei in the sporoplasm. I have recently found two sporoplasm nuclei in this microsporidian by employing Feulgen's nucleal reaction, thus confirming my previous observation with nuclear stains (Kudo, 1916) and also the findings of Ohshima (1937).

A single nucleus was observed by Schuberg (1910) in the sporoplasm of *Plistophora longifilis.* Since that time, the same condition has been reported in the following species: *Nosema aedis* (Kudo, 1930), *N. baetis* (Kudo, 1921a), *N. cyclopis* (Kudo, 1921b), *Thelohania acuta* (Schröder,

1914), *T. corethrae* (Schuberg and Rodriguez, 1915), *T. legeri, T. indica, T. obscura* (Kudo, 1929), *T. obesa* (Kudo, 1925), *T. pyriformis* (Kudo, 1924b), *T. vandeli* (Poisson, 1924), *T. varians* (Debaisieux, 1919), *Stempellia magna* (Kudo, 1924b, 1925a), *Plistophora schubergi* (Zwölfer, 1927), *Pyrotheca incurvata* and *Cougourdella magna* (Hesse, 1935).

One or two nuclei were reported in the sporoplasm of the following species: *Nosema bombycis* (Léger and Hesse, 1907; Ohmori, 1912), *Toxoglugea mercieri* (Poisson, 1924). In *Plistophora blochmanni,* Zwölfer (1926) was inclined to believe that the mature spore was uninucleate, but became binucleate when the spore entered the host's intestine. In *Nosema nonagriae,* Schwarz (1929) saw one or two nuclei, the latter being more numerous.

Two nuclei were normally observed in the following species of Microsporidia: *Nosema apis* (Fantham and Porter, 1912; Maassen, 1912; Trappmann, 1923, 1926), *N. binucleatum* (Weissenberg, 1926), *N. bombi* (Fantham and Porter, 1912), *N. bombycis* (Kudo, 1916), *N. bryozoides* (Schröder, 1914), *N. frenzelinae* (Léger and Duboscq, 1909), *N. glossiphoniae* (Schröder, 1914), *N. nepae* (Poisson, 1928), *N. notabilis, Glugea danilewskyi* (Guyénot and Naville, 1922), *Perezia legeri, P. mesnili* (Paillot, 1929), *Thelohania ephestiae* (Mattes, 1928), and *Plistophora macrospora* (Léger and Hesse, 1916).

Since recognition of the nucleus has been, and still is, dependent on certain nuclear stainings such as Heidenhain's iron haematoxylin or Giemsa's stain, it is interesting to compare the number of nuclei seen in the sporoplasm after nuclear staining and after Feulgen's nucleal reaction:

Microsporidia	*Nuclear Staining*	*Nucleal Reaction*
Nosema apis	2 (Fantham and Porter, 1912)	2 (Jírovec, 1936a)
	1 (Kudo, 1921)	
N. binucleatum	2 (Weissenberg, 1926)	2 (Jírovec, 1936a)
N. bombycis	4 (Stempell, 1909)	2 (Ohshima, 1937)
	1-2 (Ohmori, 1912)	
	2 (Kudo, 1916)	2 (this paper)
N. bryozoides	2 (Schröder, 1914)	2 (Jírovec, 1936a)
N. cyclopsis	1 (Kudo, 1921)	1 (Jírovec, 1936a)
N. notabilis	2 (this paper)	2 (this paper)
Glugea acerinae	1 (Jírovec, 1930)	1 (Jírovec, 1930)
G. anomala	4 (Stempell, 1904)	
	1 (Weissenberg, 1913; Debaisieux, 1920)	1 (Jírovec, 1932)
G. hertwigi	1 (Weissenberg, 1913)	1 (Jírovec, 1932)
Thelohania fibrata	1-2 (Strickland, 1913)	1 (Jírovec, 1936a)
T. legeri	1 (Kudo, 1921, 1924)	1 (Jírovec, 1932)
T. mülleri	2 (Stempell, 1902)	1 (Jírovec, 1936a)
Bacillidium argoisi	2 (Léger and Hesse, 1916)	1 (Jírovec, 1936a)

Thus it appears that one or two nuclei are most commonly present in the sporoplasm of the majority of species of Microsporidia.

Concerning the mode of infection of *Sphaerospora polymorpha* by *Nosema notabilis,* nothing is known. As to how the trophozoites of *Ceratomyxa coris* become infected by *Nosema marionis,* Stempell (1919) conjectured that when the spores of the two cnidosporidians are ingested by the host fish, the amoebulae leave the spores in the host's intestine and Nosema amoebulae attack young trophozoites of *Ceratomyxa coris* in the gall bladder, since he did not see any Ceratomyxa spores infected by *Nosema marionis.* He noticed infected host trophozoites attached in groups to the bladder epithelium and considered that a small number of Nosema amoebulae was probably able to infect a large number of Ceratomyxa trophozoites through the plasmotomic divisions of the hosts.

As in the case observed by Stempell, no direct infection of developing or mature Sphaerospora spores by *Nosema notabilis* has been observed up to the present time. I am therefore inclined to think that the entrance of Nosema amoebulae into the urinary bladder of the toadfish is accomplished in a way similar to that suggested for *Sphaerospora polymorpha* (p. 33), and that the microsporidian invades the host trophozoites in the fish bladder.

Résumé of Development of *Nosema notabilis*

The development of *Nosema notabilis* as observed in the trophozoites of *Sphaerospora polymorpha* is summarized in text fig. 7. The youngest binucleate schizont (1) divides into two uninucleate schizonts (2, 3) which in turn undergo a binary fission (4-9). The schizont grows (10) and develops into a spindle-form schizont (11-13). Nuclear division (14) is followed by division into two or three binucleate spindle-form schizonts (15). A sporont (16) transforms itself directly into a sporoblast (17, 18) and develops into a spore (19). The changes between stages 19 and 1 are unknown at present.

Taxonomic Consideration

From the observations described in the foregoing sections, it is clear that the organism under consideration is a true microsporidian, which should be placed in the genus Nosema in the present taxonomic scheme (Kudo, 1924a; Jírovec, 1936a). In 1924, I summarized information concerning the Microsporidia known up to that time, and described 53 known species of the genus. In 1936, Jírovec published a list of 16 additional species of the genus reported up to 1936. Since that time 5 more species of Nosema have been described. These are *Nosema haematobium* (Jírovec, 1936b), *N. carpocapsae* (Paillot, 1938), *N.* sp. (Kudo, 1938), *N. cactoblastis* and *N. cactorum* (Fantham, 1939). Thus at present 74 species of Nosema are on record. This number includes several incompletely studied
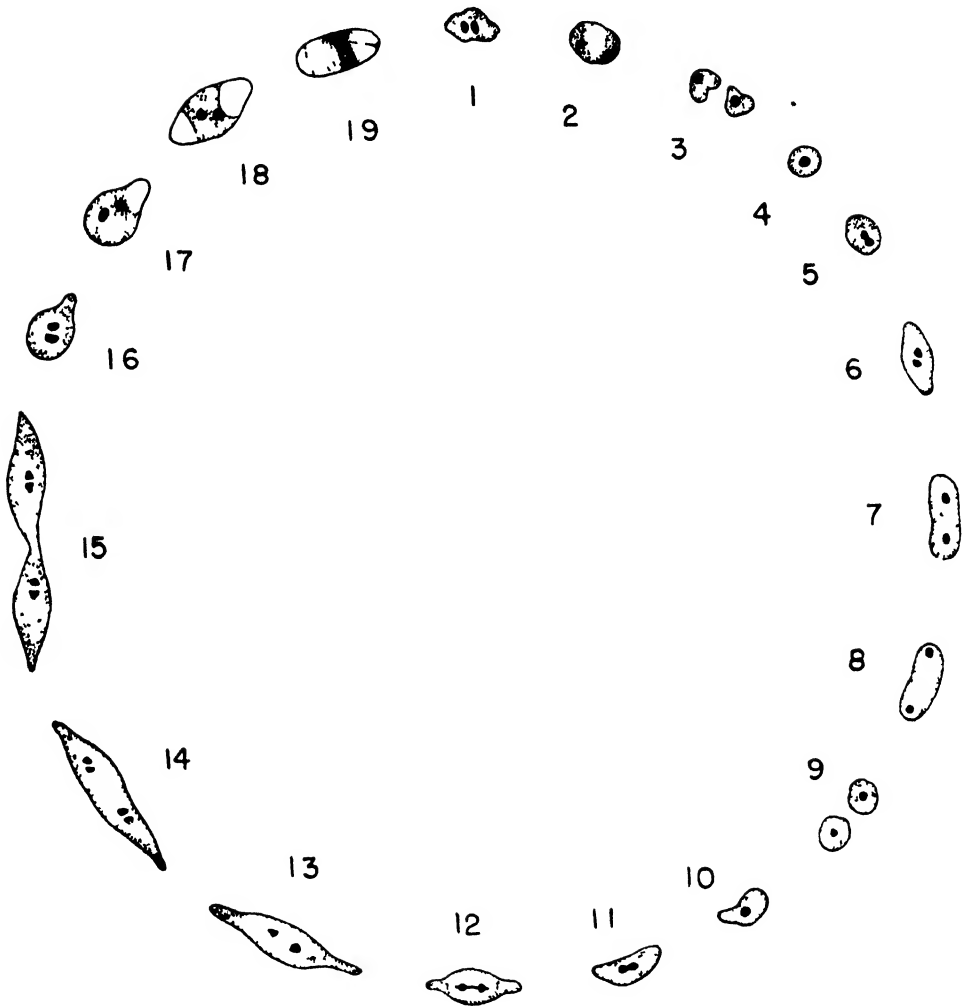
TEXT FIG 7.—Diagram showing the schizogony and sporogony of *Nosema notabilis* as seen in the trophozoites of *Sphaerospora polymorpha*.

or highly ambiguous species which may not be microsporidians at all or which may belong to other genera.

The species of Nosema are widely distributed among invertebrates and lower vertebrates. While there are a few forms such as *N. bombycis* which attacks all tissue cells of all developmental stages of *Bombyx mori* in nature and which also invades under experimental conditions at least four other lepidopterous insects (Stempell, 1909; Ohshima, 1935; Kudo and De Coursey, 1940), the majority have been found to parasitize particular tissue cells of a specific host animal. In spite of the absence of our knowledge as to how specific the host-microsporidian relationship is, the difference in the host species has to be used as one of the important bases

in the identification of the microsporidian species. In *Nosema notabilis,* the association of the host and the parasite is so unique and unusual that the specific relationship between the two protozoans may be emphasized.

Comparison of *Nosema notabilis* with other recorded species in the genus shows that it differs in host association and in characteristics of the spore and developmental stages. Special attention, however, must be given to a comparison between it and *Nosema marionis,* for both are parasitic in the trophozoites of coelozoic myxosporidians in marine fishes.

N. marionis was first discovered by Thélohan (1895) in the gall bladder of *Coris julis* and *C. giofredi* at Marseille. Apparently, as pointed out by Stempell later, there were present no spores of a myxosporidian observed by Georgévitch (1917). Thélohan assumed the whole amoeboid organism, with an average diameter of 40 to 55 μ, a microsporidian trophozoite, and named it *Glugea marionis.* Thélohan characterized the spores by stating: "en forme d'ovoide très allongé; très peu atténuées en avant; la largeur est comprise deux fois et demie dans la longueur. Longueur 8 μ, largeur 3 μ." Georgévitch (1917) also observed a microsporidian in the same organ of the same host fishes which he thought was identical with what Thélohan had described. Finding elongate fusiform spores in the cytosome of sporulating trophozoites of *Ceratomyxa coris,* he maintained that the two cnidosporidians underwent accidental plasmogamy, but did not state whether the two organisms lived separately and independently also. Finally, Stempell (1919), who studied the two cnidosporidians in the same two host fishes, came to the conclusion that the microsporidian was a species of Nosema and that it was parasitic in the cytosome of the myxosporidian. The spores were elongate-oval, with or without a clear rounded space at one end, and varied in length from 1.5 to 7 μ. The width is not given, but the figures of the spores given by Stempell (1919: figs. 77-79) are similar to those figured by Thélohan. Stempell stated that its development was similar on the whole to that of *Nosema bombycis,* quoted before.

In being a parasite in myxosporidians, *Ceratomyxa coris* and *Sphaerospora polymorpha,* respectively, *Nosema marionis* (Thélohan) and the present species are alike, but resemblances stop there, for the chief characteristics of the spores and schizogonic changes differ too greatly between them. Moreover, *Ceratomyxa coris* has been an exclusive inhabitant of the gall bladder of two species of Coris in European waters, while *Sphaerospora polymorpha* inhabits the urinary bladder of the toadfish in North American waters. Therefore, the microsporidian described in detail here was considered a new species and was named *Nosema notabilis* in 1939.

Diagnosis of *Nosema notabilis* Kudo

Host.—Trophozoites of *Sphaerospora polymorpha* Davis, inhabiting the urinary bladder of *Opsanus tau* and *O. beta*.

Locality.—Chesapeake Bay, Solomons Island, Maryland; Lemon Bay, Englewood, Florida.

Trophozoite.—Young forms (1.5-2 μ in diameter) binucleate, amoeboid; binary fission results in production of two uninucleate schizonts which grow and in turn undergo binary fission. Schizonts develop into binucleate spindle-form schizonts which divide. Divisions are seemingly repeated. A binucleate sporont transforms itself into a sporoblast, and this in turn develops into a binucleate spore.

Spore.—Ovoid to ellipsoid, with unequally rounded ends; with or without a rounded space, or "vacuole," at the more rounded extremity. Spore membrane is of one piece. Binucleate sporoplasm is a girdle-form ring. Polar filament is attached at a point near the tip of the narrower end and spirally coiled in the intrasporal space, the coil not reaching the posterior extremity. Fresh spores measure 2.9-4 μ long by 1.4-2.5 μ wide. The smallest spores were 2.9 by 1.4 μ; the largest, 4.8 by 2 μ. When extruded, the polar filament reaches a length of 45-62 μ.

Remarks.—When lightly infected, the spore formation in the host trophozoites proceeds more or less normally; when infection is severe, the host nuclei undergo hypertrophy and degeneration, and no spore formation takes place. The microsporidian is therefore considered as a pathogenic parasite of the myxosporidian.

VI. SUMMARY

(1) Eighty-two toadfish (*Opsanus tau* and *O. beta*) obtained from Maryland and Florida were all found to harbor in their urinary bladders a coelozoic myxosporidian, *Sphaerospora polymorpha* Davis, which in turn was infected by a microsporidian, *Nosema notabilis* Kudo.

(2) The infection of *Sphaerospora polymorpha* by *Nosema notabilis* is the fifth case of hyperparasitism known up to the present time, in which a parasitic protozoan is infected by a microsporidian.

(3) The urinary system of *Opsanus tau* and *O. beta* shows a distinct sexual dimorphism. In the male, the urinary bladder has two horns, the left being larger than the right, while in the female there is only the left horn.

(4) *Sphaerospora polymorpha* was found exclusively in the urinary bladder. The trophozoites are mostly attached to the bladder epithelium in scattered groups or in one to several layers. The cytosome of the

bladder epithelial cells is destroyed by the parasites, but the host nuclei are little affected.

(5) The trophozoites multiply by a simple and possibly multiple plasmotomy. The generative nuclei divide by mitosis, in which four chromosomes become apparent, while the vegetative nuclei multiply by amitosis.

(6) The generative nuclei undergo meiotic division in which the two daughter nuclei receive two chromosomes each. Two such cells unite and form a sporont (or pansporoblast), but the two nuclei remain separate. The smaller nucleus divides once, while the larger nucleus multiplies repeatedly until twelve nuclei, all haploid, are formed. The sporont now differentiates into two sporoblasts, which in turn develop into two spores. The two haploid sporoplasm nuclei fuse into a single diploid nucleus before further development takes place.

(7) *Sphaerospora polymorpha* is compared with other known species of the genus and a diagnosis of the species is given.

(8) *Nosema notabilis* is an exclusive parasite of *Sphaerospora polymorpha*. In severely infected host myxosporidians, the generative nuclei are hypertrophied and degenerated, and no spore-formation takes place. *Nosema notabilis* is a true parasite of *Sphaerospora polymorpha*.

(9) Schizogony is by binary fission. No sexual process has been observed in the development of *Nosema notabilis*. The spore possesses a binucleate sporoplasm, and the spore membrane is of a single piece. A modification of previously reported methods for extrusion and observation of the polar filament is described.

(10) *Nosema notabilis* is compared with the known species of Nosema and its diagnosis is given.

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EXPLANATION OF PLATES

The drawings were made by means of Abbe's drawing apparatus. The photomicrographs are untouched enlargements of negatives obtained with a Phoku camera. The abbreviations used in the descriptions of figures are as follows:

B........Bouin fixation.
C........Carnoy fixation.
F........Feulgen's nucleal reaction.
G........Giemsa staining.
H ....Heidenhain staining.
M ....Methyl alcohol fixation.
S........Schaudinn fixation.
Sec......Serial section preparation.
Sm......Smear preparation.

PLATE I

Sphaerospora polymorpha; figs. 1-9 × 2300; figs. 10-19 × 1060.

FIGS. 1-6.—Typical appearances of small trophozoites as seen in life in Nemeczek hanging drop preparations.

FIG. 7.—Large trophozoite with two developing spores in life.

FIGS. 8-9.—Small trophozoites infected by *Nosema notabilis* in life.

FIG. 10.—Small trophozoite treated with Sudan III, showing fat globules.

FIG. 11.—Group of eight small trophozoites in life.

FIGS. 12-16.—Trophozoites of different sizes and appearances as seen in life

FIG. 13.—Trophozoite in the act of engulfing a spore in life.

FIG. 14.—Disporous trophozoite in life.

FIG. 15.-- Polysporous trophozoite in life.

FIG. 16.—Trophozoite with engulfed foreign bodies which were present in numbers in the urine.

FIGS. 17-18.--Two stages in plasmotomy in life.

FIG. 19.—Abnormal fresh spore containing four polar capsules.
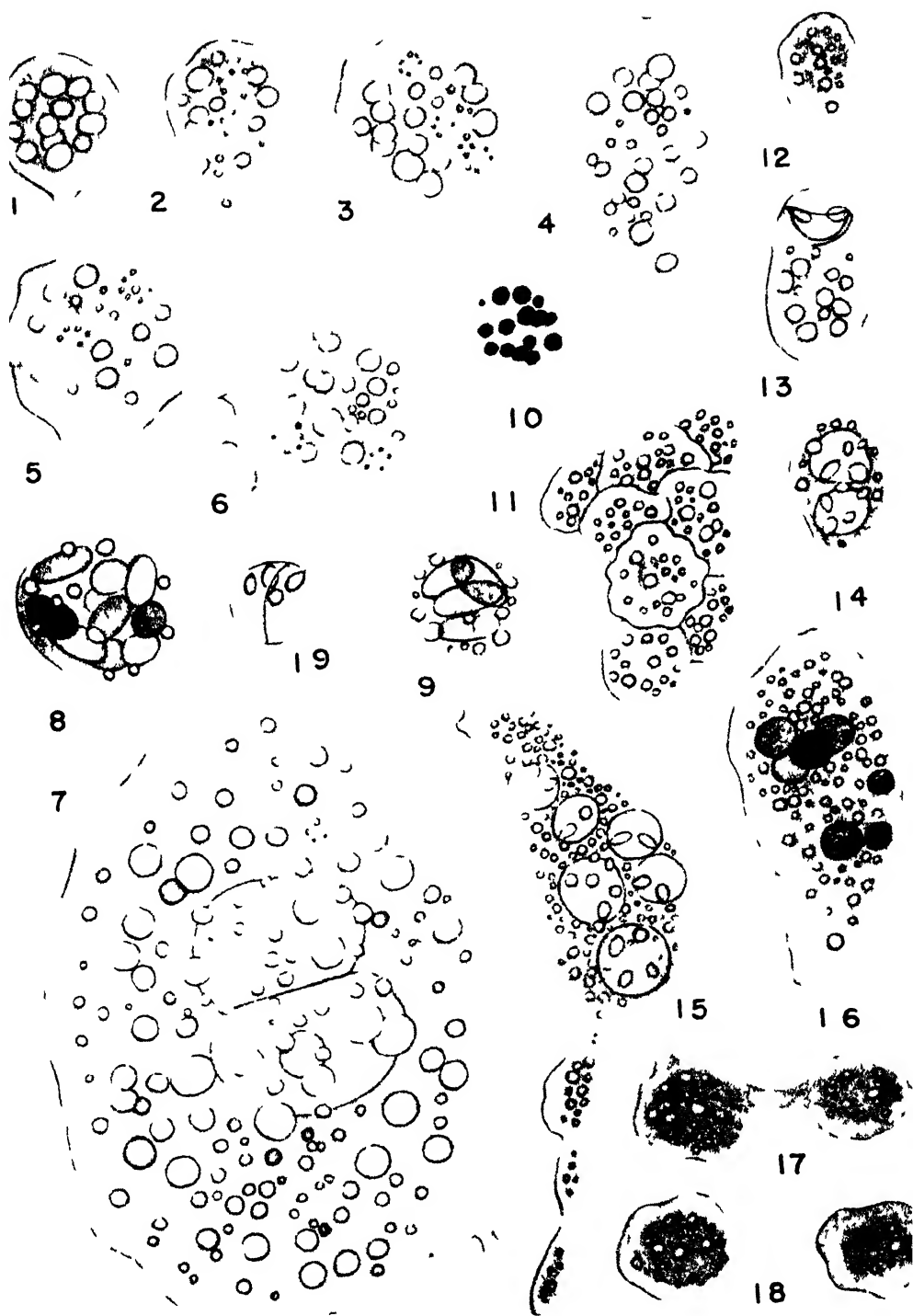
PLATE I

PLATE II

Sphaerospora polymorpha; × 2100.

FIG. 20.—Uninucleate trophozoite. Sm.S.G.

FIGS. 21-22.—Small trophozoites with a generative and a vegetative nucleus. Sm.S.G.

FIG. 23.—Binucleate trophozoite in which the generative nucleus is undergoing division (prophase). Sm.S.G.

FIG. 24.—Trinucleate trophozoite, with one vegetative and two generative nuclei. Sm.S.G.

FIG. 25.—Similar trophozoite. Sm.B.H.

FIG. 26.—Tetranucleate trophozoite; one of the two vegetative nuclei is dividing by amitosis. Sm.S.G.

FIG. 27.—Trophozoite with 2 generative and 4 vegetative nuclei. Sm.S.G.

FIG. 28.—Trophozoite with 4 generative nuclei and a vegetative nucleus. One of the generative nuclei is dividing (metaphase). The cytoplasm contains a foreign body of homogeneous substance. Sm.S.G.

FIG. 29.—Multinucleate trophozoite with one dividing generative nucleus at anaphase and with 3 engulfed foreign bodies. Sm.S.F.

FIGS. 30-31.—Upper and lower level views of a trophozoite in which two spores are nearly mature. Sm.S.G.

FIG. 32.—Generative nucleus in early prophase. Sec.S.F.

FIG. 33.—Prophase. Sec.C.H.

FIGS. 34-35.—Prophase. Sec.S.F.

FIG. 36.—Metaphase in polar view (?). Sec.S.F.

FIGS. 37-39.—Metaphase. Sec.C.H.

FIG. 40.—Anaphase. Sec.C.F.

FIGS. 41-42.—Anaphase. Sec.C.H.

FIG. 43.—Telophase. Sec.C.H.

FIGS. 44-45.—Telophase. Sec.S.F.
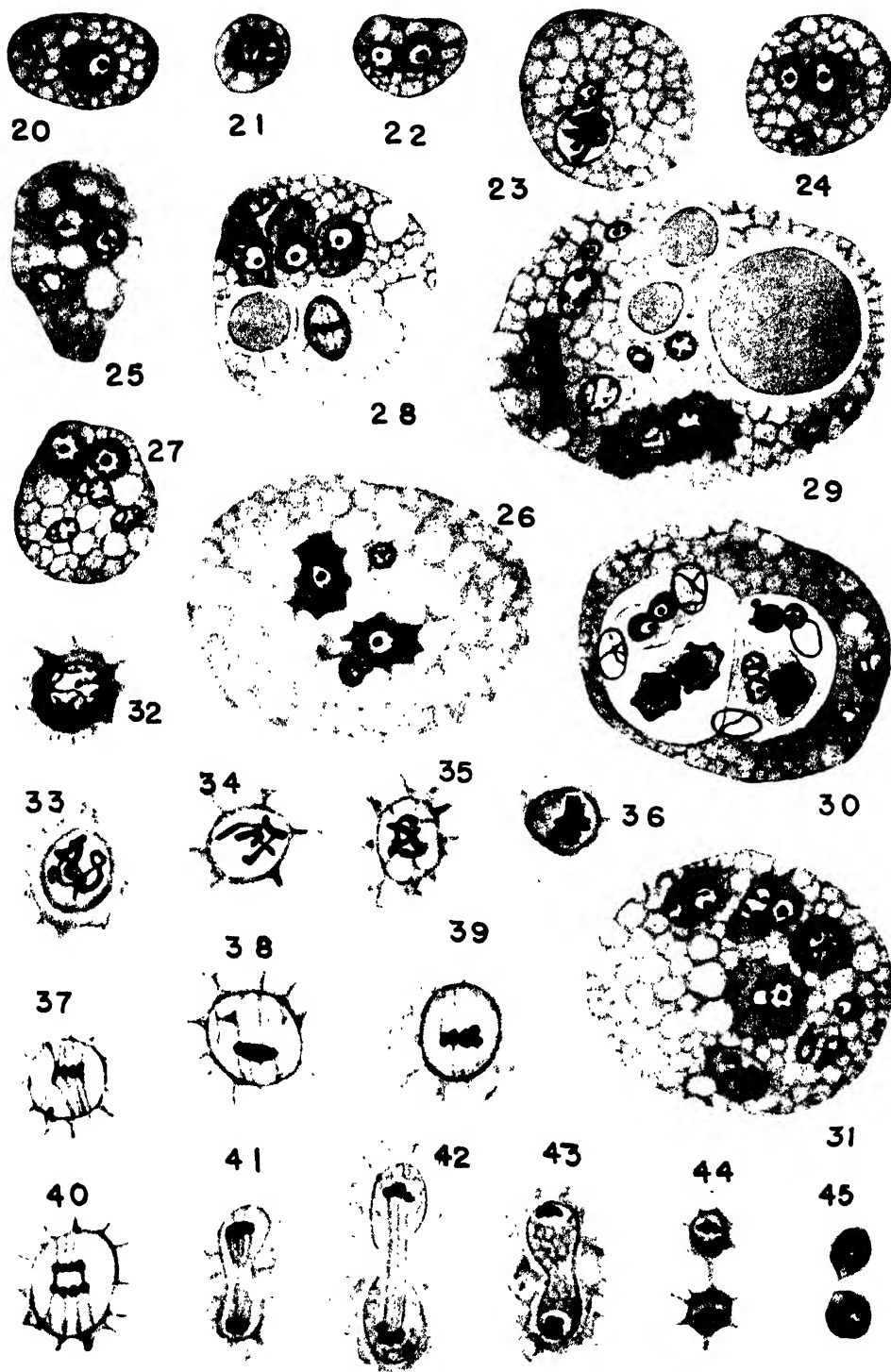
PLATE II

PLATE III

Sphaerospora polymorpha; × 2100.

FIGS. 46-54.—Meiotic division stages of the generative nucleus:
    46-47—Prophase, Sm.S.G.   52—Telophase, Sec.S.F.
      48—Metaphase, Sec.S.F.   53-54—Telophase, Sm.S.G.
    49-51—Anaphase, Sec.S.F.

FIGS. 55-57.—Association of two uninucleate generative cells, to form a sporont
    or pansporoblast: 55—Sec.C.H.; 56—Sec.S.H.; 57—Sm.B.H.

FIGS. 58-78.—Nuclear divisions and development of sporonts:

58-59—Sm.B.H.	68—Sec.C.H.	75—Sm.S.G.
60-61—Sec.C.H.	69—Sm.B.H.	76—Sec.C.H.
62—Sm.B.H.	70-71—Sec.S.F.	77-78—Sec.S.F.
63-66—Sec.C.H.	72—Sm.S.F.	
67—Sm.B.H.	73-74—Sec.C.H.	

46   47   48   49   50   51

52   53   54   55   56   57

58   59   60   61   62   63

64   65   66   67   68   69

70   71   72   73   74

75   76   77   78
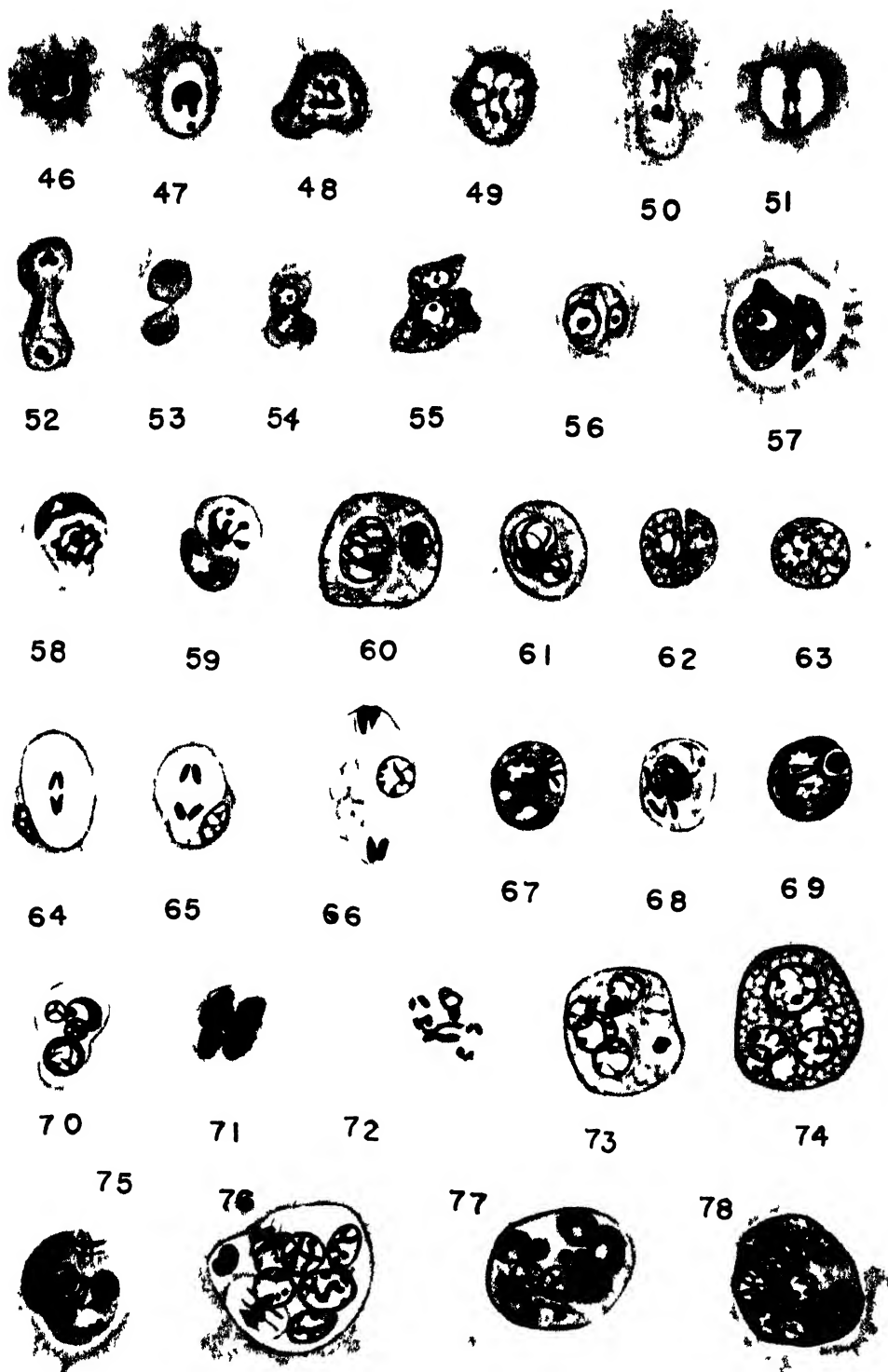
PLATE III

PLATE IV

Sphaerospora polymorpha; × 2100.

FIG. 79.—Late stage of developing sporont. Sm.S.G.

FIG. 80.—A nearly completely developed sporont, with two sporont nuclei and two young spores. Sm.S.F.

FIG. 81.—More mature spores. Sec.S.F.

FIG. 82.—Young spore. Sm.S.G.

FIG. 83.—Unusually large nearly mature spore. Sm.S.F.

FIGS. 84-85.—Two views of two almost fully formed spores. Sec.S.F.

FIG. 86.—A young spore from which the binucleate sporoplasm has been forced out. Sm.S.G.

FIGS. 87-88.—Surface views of two developing spores in which striae are being formed. Sm.S.G.

FIG. 89.—Mature spore. Sm.S.F.

FIG. 90.—Mature spore with a single nucleus in the sporoplasm. Sm.S.F.

FIG. 91.—Small spore in optical section. Sm.S.G.

FIG. 92.—Portion of a spore which has been subjected to mechanical pressure, showing the striae on the membrane. Sm.S.G.

FIG. 93.—Spore which was kept air-dried for two weeks and which extruded one of the filaments under the influence of potassium hydrate. Sm.S.G.

FIGS. 94-95.—Optical section views through the polar capsules of two fresh spores as seen in the host's urine.

FIG. 96.—Slightly oblique front view of a fresh spore.

FIGS. 97-98.—Anterior end views of two fresh spores.

FIG. 99.—Lateral surface view of a fresh spore.

FIGS. 100-104.—Abnormal spores in life.
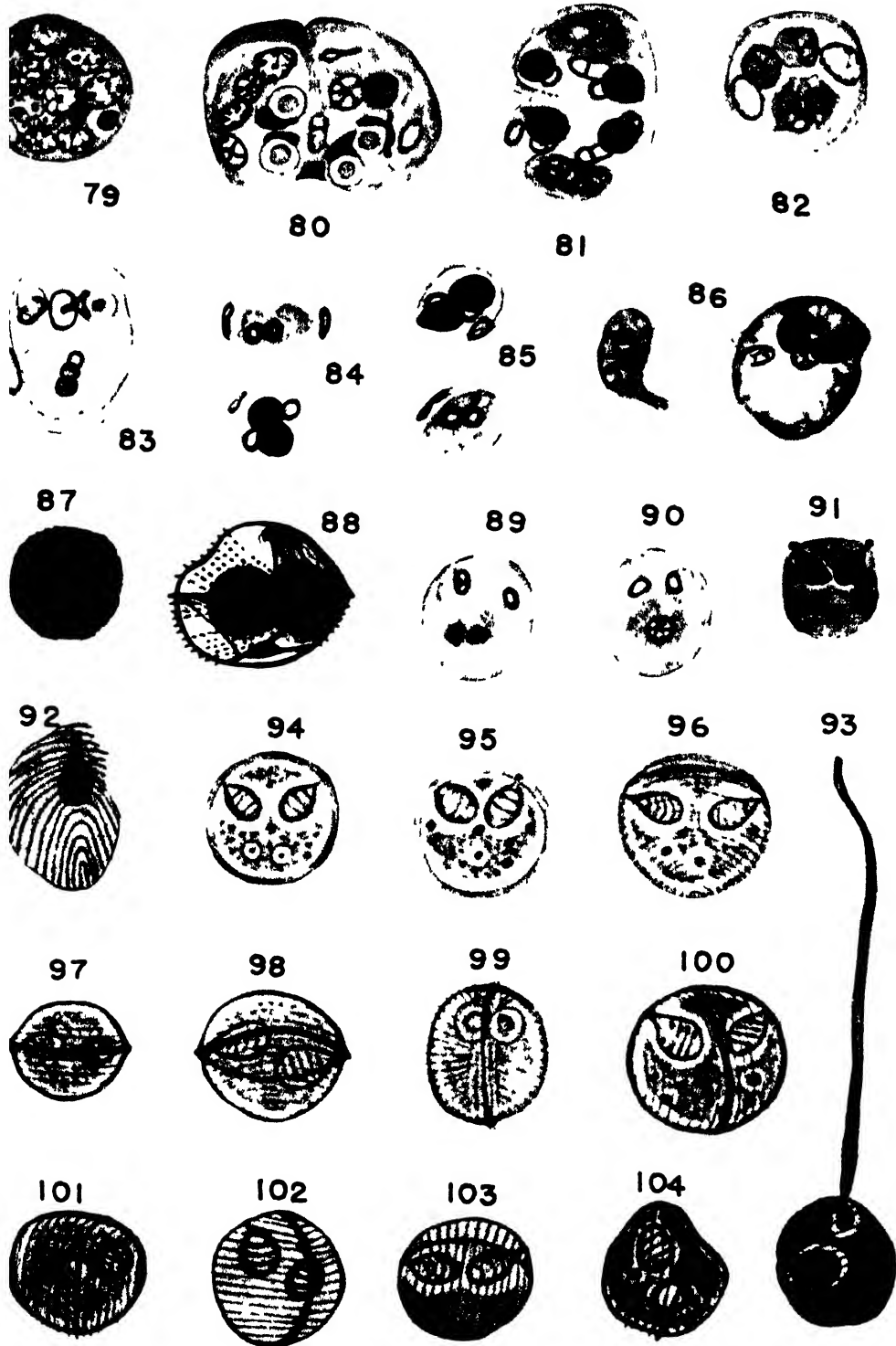
PLATE IV

PLATE V
Nosema notabilis; × 2100.

Fig. 105.—Eight fresh spores, showing different forms and dimensions.

Fig. 106.—Two different views of a single fresh spore.

Fig. 107.—Four pyriform fresh spores.

Fig. 108.—Two spores stained deeply. Sm.S.H.

Fig. 109.—A spore more decolorized. Sm.S.H.

Fig. 110.—An optical section of a similarly treated spore. Sm.S.H.

Fig. 111.—Two mature spores. Sec.S.F.

Fig. 112.—Optical section of a spore. Sec.S.F.

Fig. 113.—Five spores found in different host fish. Sm.S.G.

Figs. 114-115.—Two spores with partially extruded polar filaments under mechanical pressure. Sm.M.G.

Fig. 116—Young binucleate trophozoite. Sm.S.G.

Figs. 117-120.—Stages in binary fission of binucleate schizont. Sm.S.G.

Figs. 121-127.—Stages in binary fission of uninucleate schizonts: 121-122, Sm.S.G.; 123, Sm.S.F.; 124-125, Sec.C.H.; 126, Sec.S.F.; 127, Sec.C.H.

Figs. 128-136.—Stages in the development of spindle-form schizonts: 128-133, Sm.C.H.; 134-136, highly spread out schizonts, Sm.S.G.

Figs. 137-141.—Further division of spindle-form schizonts: 137-140, Sm.C.H.; 141, Sec.S.G.

Figs. 142-144.—Stages in sporont-formation. Sm.C.H.

Figs. 145-146.—Sporoblast and young spore. Sm.S.G.

105

106 · 107

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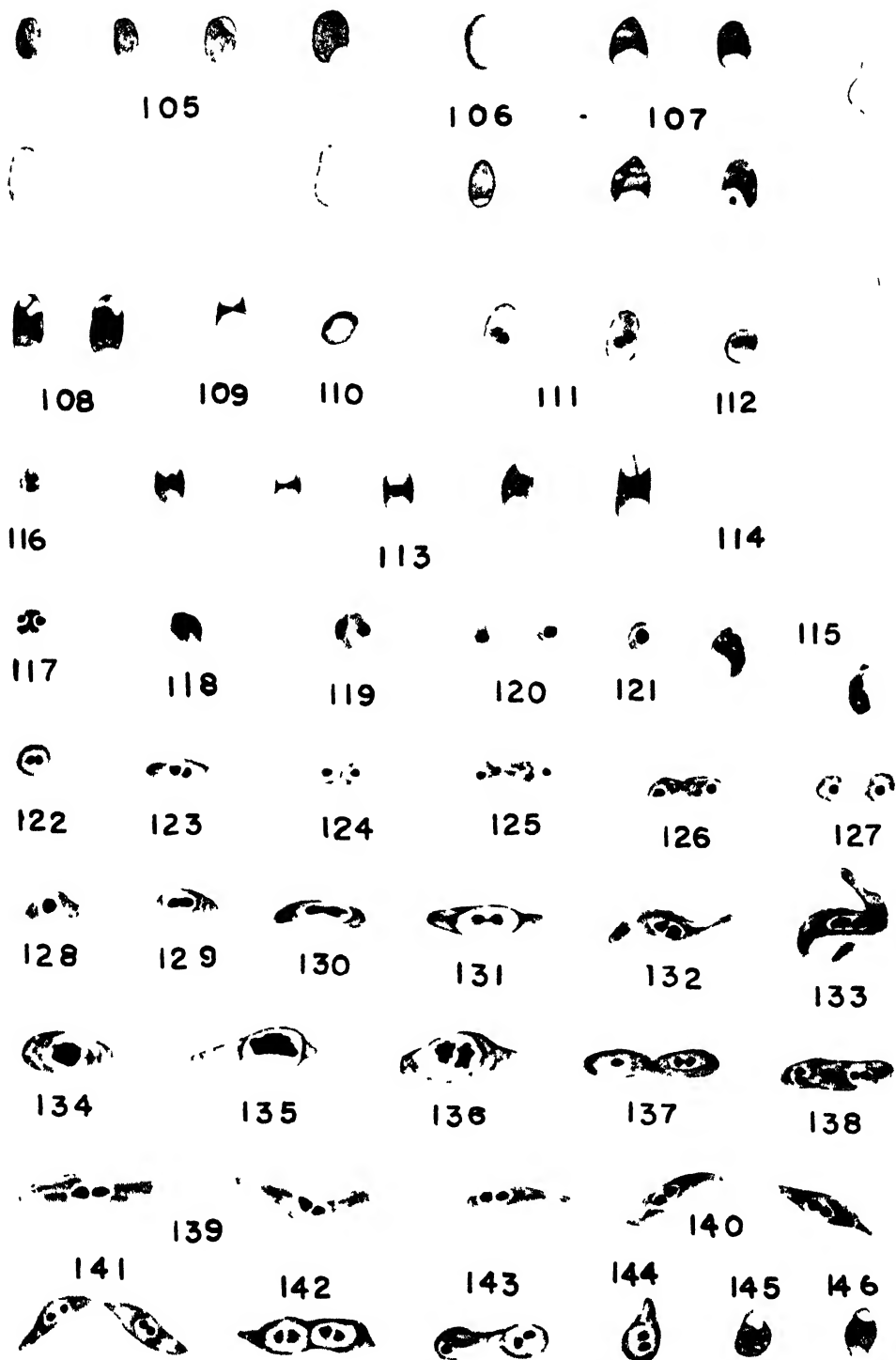
PLATE V

PLATE VI

Sphaerospora polymorpha infected by *Nosema notabilis;* × 2100.

FIG. 147.—Young binucleate host trophozoite infected by five Nosema schizonts. Sm.S.G.

FIG. 148.—Tetranucleate trophozoite with eight Nosema schizonts. One host nucleus is extremely hypertrophied. Sm.S.G.

FIG. 149.—Small trinucleate trophozoite with six Nosema schizonts. Sm.S.G.

FIG. 150.—Trinucleate trophozoite infected by nine uninucleate Nosema schizonts. The three host nuclei are degenerated. Sm.S.G.

FIG. 151.—Larger trophozoite. The host nuclei are beginning to become hypertrophied. Sm.S.G.

FIG. 152.—Trophozoite lightly infected by six binucleate schizonts and a young spore of Nosema. Sm.S.G. See also fig. 171.

FIG. 153.—Another lightly infected trophozoite with thirteen Nosema schizonts. Sm.S.G. See also fig. 172.

FIG. 154.—Heavily infected trophozoite with eight somewhat hypertrophied and degenerating nuclei, filled with ten schizonts and twenty-two spores of Nosema. Sm.S.G. See also fig. 173.

FIG. 155.—Moderately infected trophozoite. Sec.S.F.

FIG. 156.—Trophozoite with twelve schizonts and two young spores of Nosema. The host nuclei appear normal. Sec.C.H.

FIG. 157.—More heavily infected host trophozoite. Sec.C.H.

FIG. 158.—Small trophozoite with nine spores and two schizonts of Nosema. Three host nuclei have degenerated. Sm.S.G.

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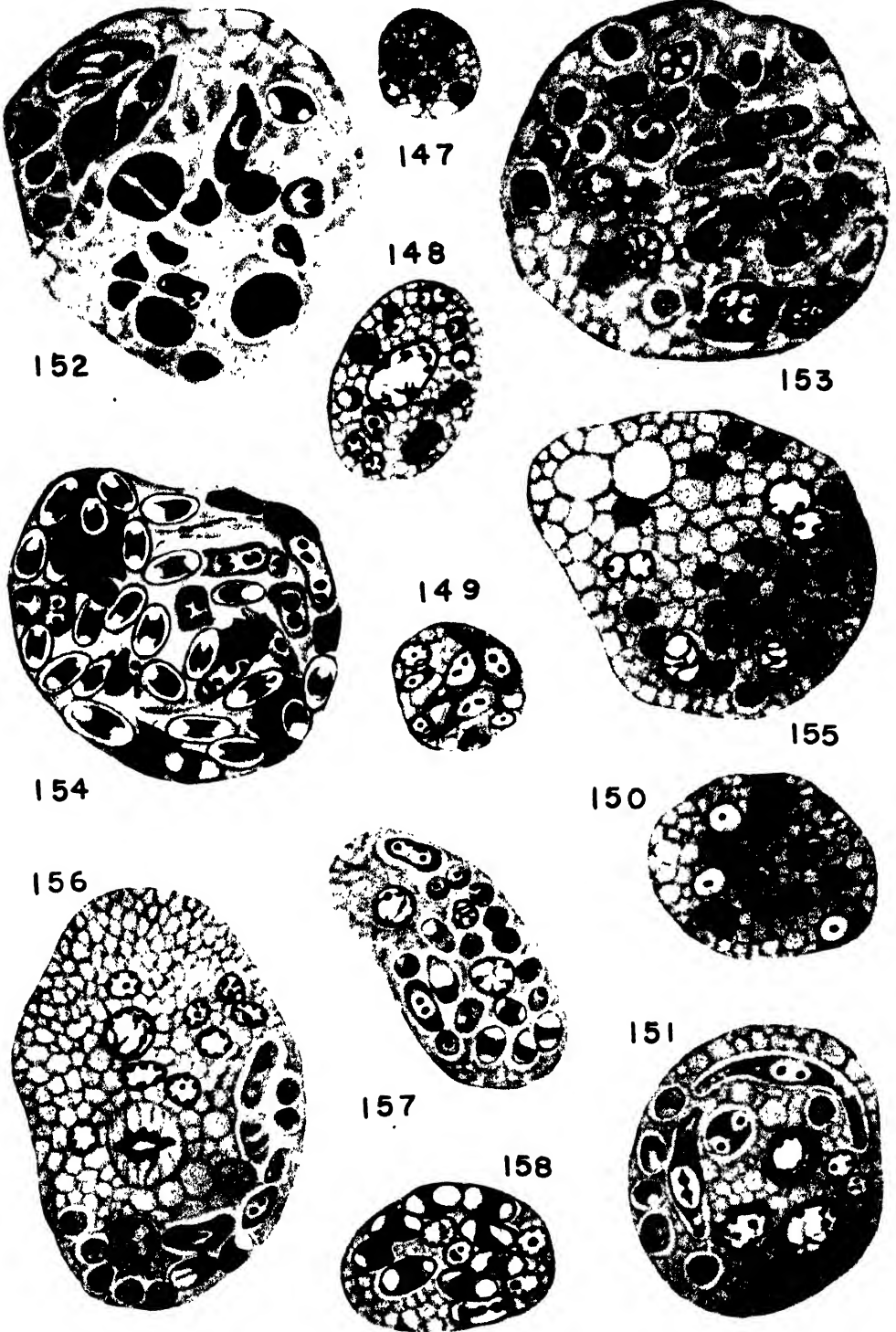
PLATE VI

PLATE VII

Fig. 159.—Fresh scraping of the wall of the urinary bladder of a toadfish, showing trophozoites and isolated spores of *Sphaerospora polymorpha*. The microsporidian spores are indistinctly visible. Life, × 470.

Fig. 160.—Trophozoite of *Sphaerospora polymorpha*, crushed under the cover glass, showing 21 spores of *Nosema notabilis* which developed within, and at the expense of, it. Life, × 2100.
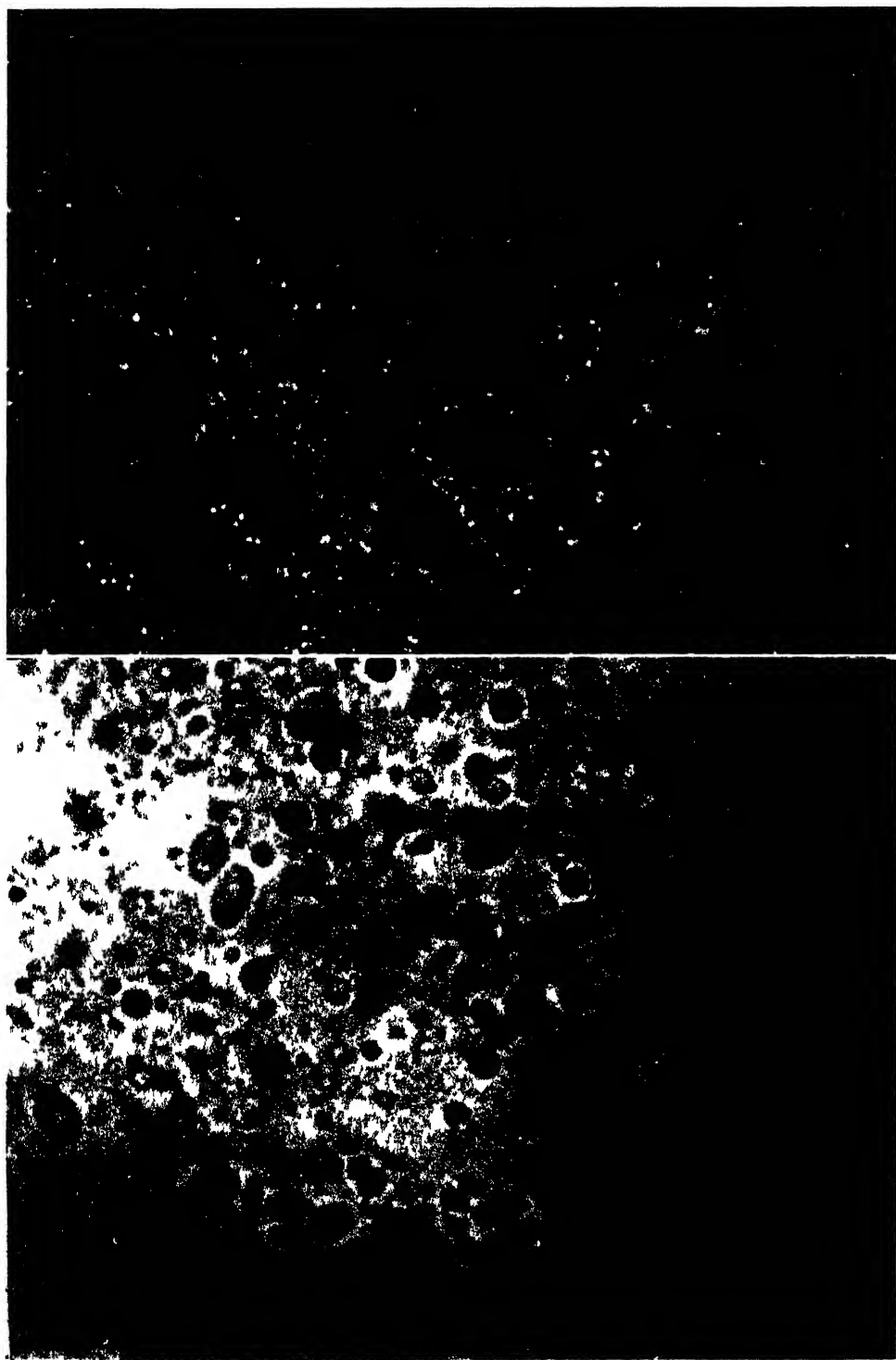
PLATE VII

PLATE VIII

FIG. 161.—Portion of the bladder epithelium of a toadfish with attached elongated trophozoites of Sphaerospora, three of which contain mature spores. Sec.S.G. × 470.

FIG. 162.—Portion of the urinary bladder of another fish, very heavily infected by *Sphaerospora polymorpha*, many of which are infected by Nosema. Sec.C.H. × 470.
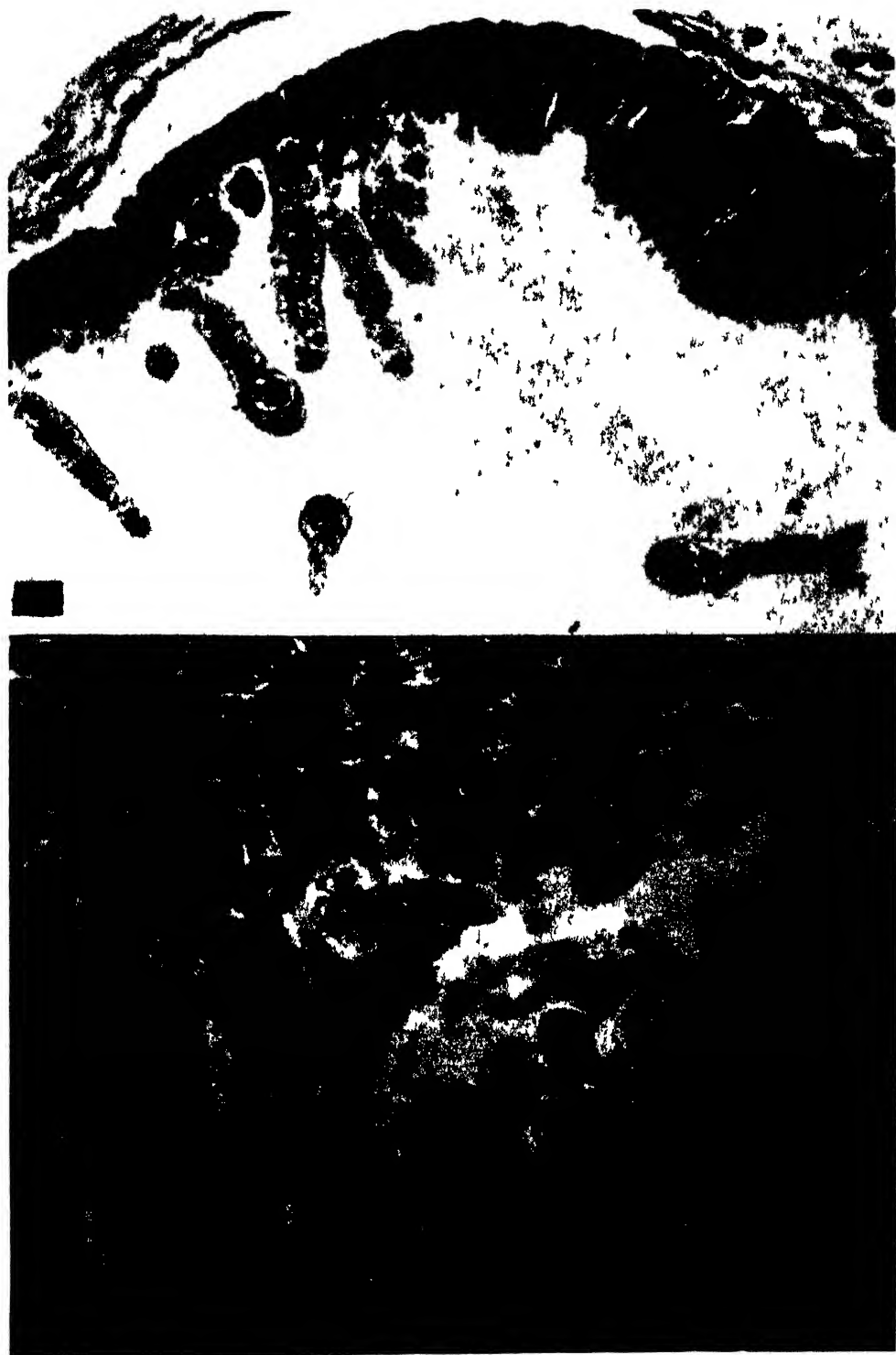
PLATE VIII

PLATE IX

FIG. 163.—Portion of the urinary bladder of a toadfish, showing eleven tropho-
zoites of *Sphaerospora polymorpha*, three of which are heavily in-
fected by *Nosema notabilis*. Sec.S.H. × 2100.

PLATE IX

PLATE X

FIG. 164.—Portion of a urinary bladder containing 12 Sphaerospora trophozoites, heavily infected by schizonts, sporonts, and spores of Nosema. Sec.S.G. × 1575.

PLATE X

PLATE XI

FIGS. 165-170.—Spores of *Noscma notabilis* with their extruded polar fila-
ments under the influence of hydrogen peroxide or of mechanical
pressure. All dark field, except fig. 167. × 1575. Figs. 166 and 167
are dark field and bright field views of the same spore. Note the
faintly visible basal portion of the extruded filament in fig. 167.

PLATE XI

PLATE XII

Fig. 171.—Sphaerospora trophozoite shown in fig. 152. × 2050.
Fig. 172.—Sphaerospora trophozoite shown in fig. 153. × 2050.
Fig. 173.—Sphaerospora trophozoite shown in fig. 154. × 2050.
Fig. 174.—Sphaerospora trophozoite heavily infected by Nosema. Sm.S.G.
      × 2100.
Fig. 175.—Portion of the urinary bladder of a toadfish with Sphaerospora tro-
      phozoites which are all heavily infected by Nosema. Sec.S.G.
      × 1150.
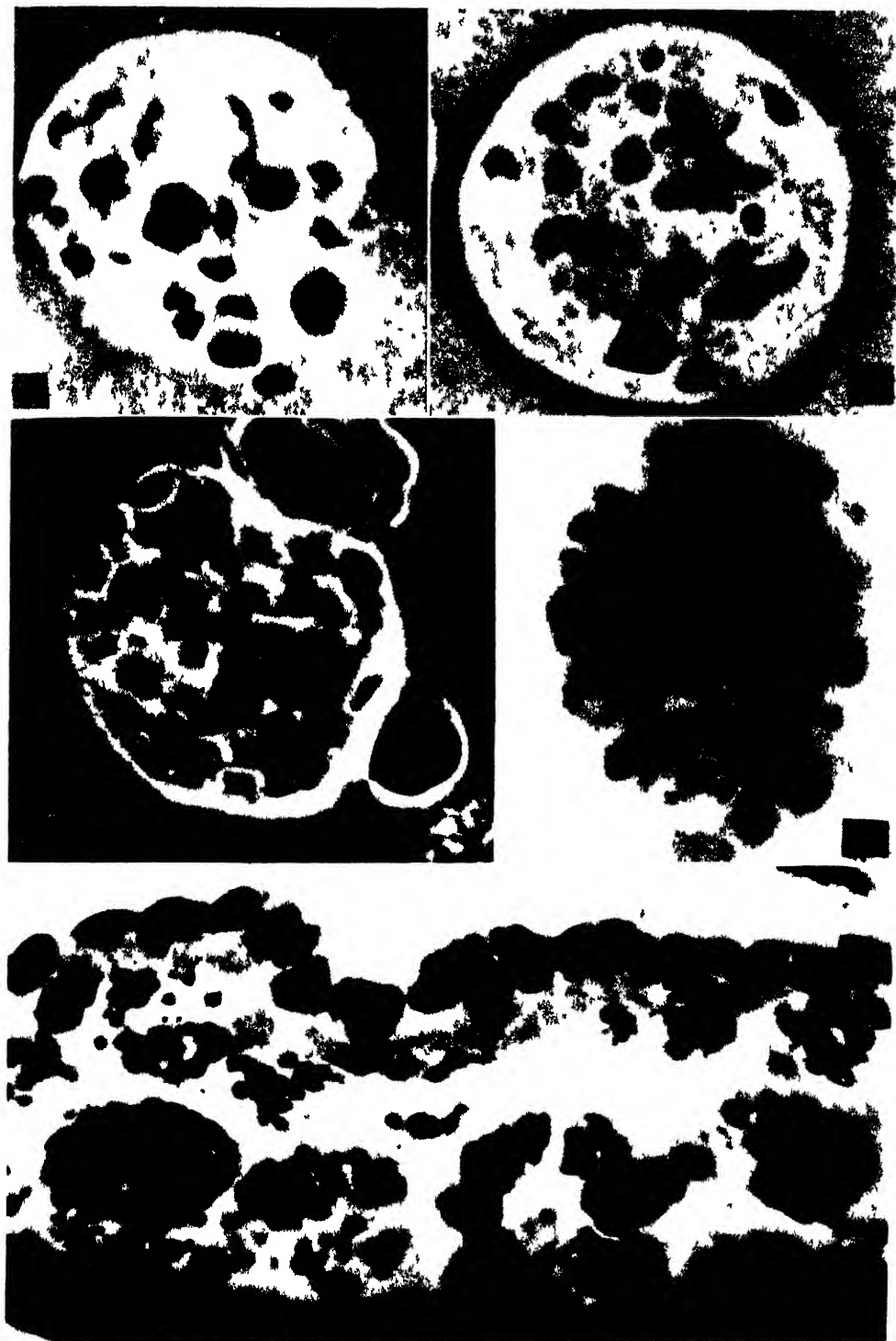
PLATE XII

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XX   No. 2

AMERICAN SPECIES OF AMELANCHIER

WITH 14 MAPS AND 23 PLATES

BY

GEORGE NEVILLE JONES

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CONTENTS

I. INTRODUCTION

AMELANCHIER is a genus of shrubs and small trees belonging to the subfamily Pomoideae of the Rosaceae and including not more than two dozen species widely distributed in North America, Europe, northern Africa, and eastern Asia. Some kinds are highly ornamental and are planted for the showy early white flowers, as well as occasionally for the more or less edible fruits. Only the American species are included in this paper. Their number is eighteen. Two others formerly included in Amelanchier, inhabiting Guatemala and Mexico (and southern Texas), have been transferred to the genus Malacomeles, and are treated in another paper.

The origin of the generic name Amelanchier is not definitely known, but probably it has been derived from the Provençal name of the European *Amelanchier ovalis* Medic. The American amelanchiers are known by the common names serviceberry, sarviceberry, sarvis, maycherry, juneberry, shadblow, shadbush, shadberry, shadblossom, shadflower, shadwood, sugar pear, wild pear, lancewood, boxwood, Canadian medlar, bilberry, snowy mespilus, saskatoon, and perhaps some others. These vernacular names are used as follows: serviceberry, because of the similarity of its fruit to that of the European service tree (*Sorbus torminalis* (L.) Crantz); juneberry because the berry-like fruits of certain species ripen in June; in the eastern part of the United States the names shadblow, shadberry, shadblossom, shadflower, and shadwood are used for certain species that are in bloom when shad begin to ascend the streams. Lancewood and boxwood have been applied to other species because their wood has been used for handles for tools. The name saskatoon, used in western Canada for the fruits of *Amelanchier alnifolia* Nutt. and the bushes on which they grow, originated with the Blackfoot Indians, who used the fruits either fresh or dried. The pemmican of the Indians was composed of dried and pulverized deer or buffalo meat to which was added saskatoon berries, the mixture then being stirred into boiling fat, and when cooled molded into cakes. Explorers and prospectors found the fruits a welcome addition to their food supply, and it is recorded that the fruit of *A. alnifolia* was used by the members of the Lewis & Clark Expedition when they ran short of other food. The foliage of some of the western species is a palatable forage for grazing animals. Some of the eastern species make a satisfactory stock on which to graft the pear and quince.

The species of Amelanchier are closely related and are sometimes somewhat difficult to distinguish. One or more is found in each province of Canada, and in every state in the United States. The earlier students of the North American flora, including Michaux, Pursh, Nuttall, Torrey, and Gray, took the view that the genus in the western hemisphere con-

sisted of only one, or at the most very few, highly variable species. This attitude characterized the understanding of the genus in the United States during the greater part of the nineteenth century. Subsequent students have, however, broken away from this viewpoint, and there now may be found in botanical literature nearly two hundred binomials and trinomials representing the species of Amelanchier in America.

In 1912 the late Professor K. M. Wiegand, of Cornell University, presented a tentative revision of Amelanchier in eastern North America, recognizing eight species, including three newly described by himself. Subsequently, he described three more. His work has been followed rather closely by almost all recent writers of manuals, floras, and check-lists. It now appears that some species were improperly typified, and that the assumption was made that some of the nomenclatural types were "hybrids" and therefore to be discarded. This policy has been the cause of a certain amount of confusion in the taxonomy and nomenclature of several species. Probably this inexact typification was at least partly responsible for the vagueness and haziness of the specific lines, with the result that many specimens were supposed to belong to hybrid plants rather than to true species. In later years, Wiegand (Science, n.s. 81:161-166. 1935) concluded that there are in eastern North America

. . . six or seven good species with normal ranges coinciding in general with the geographical areas in eastern North America, and fitting in with the ranges of other plants. The hybrids were usually local. Circumstantial evidence, therefore, seemed to indicate that these true species had been in existence a long time, during which they had spread over wide areas, as for instance from Newfoundland to Georgia and Minnesota — over all the area having suitable habitat conditions. They were old enough to have become more or less static as far as distribution was concerned. The hybrids seem like swarms of bees, buzzing around for a time, only to disappear, leaving the fundamental species to continue through the ages. . . . It can not be denied that species may have arisen through hybridity, quite possibly in the ways suggested by many geneticists, but one can not become very enthusiastic. At least, it seems evident that species are not being formed every day, or even every year, or even every century, as some enthusiasts are inclined to think.

In the genus Amelanchier, as in many other genera of vascular plants, hybridization between different species doubtless sometimes occurs, and the hybrids are recognizable by those familiar with the species, but as Wiegand has already pointed out the hybrids constitute an insignificant element in the flora. Referring to the subject of hybridization in Rubus, Dr. L. H. Bailey (Gentes Herbarum 2:272, 273. 1932) writes as follows:

We do not elucidate the blackberry problem by the assumption of miscellaneous hybridity as if the species themselves were known and all the puzzles were mixed progeny: our work takes a new direction the moment we cease to invoke crossing as a way to escape from difficulties. The fact that certain forms are puzzling and of doubtful specific validity does not make them hybrids. Hybrids there may be, but the first effort is to determine the species which are supposed to spawn into mongrels. Hybridity is to be accepted only on evidence; it can not be determined by the examination of usual herbarium specimens.

Recent trends in taxonomic studies of vascular plants emphasize the importance of exact typification and detailed diagnosis and description, as well as critical examination of a large series of specimens from the total geographical area of each species. Through the application of this method it is usually possible to outline a much more precise concept of the specific entities, and to interpret more accurately the boundaries between species, than was possible in former times. The net result of this sharper delineation is that the number of puzzling "intermediates," "hybrids," "varieties," "forms," and other taxonomic *collectanea* is appreciably diminished.

In a recent study (Gentes Herbarium 5:912, 913. 1945), Bailey says:

The office of taxonomy is to distinguish and define the units, which we call genera and species, and then to name the units so that they may be assembled into larger classes: the word taxonomy signifies classification. When we confuse the definitions we obscure the program. Taxonomy is not primarily the discovery of all detectable differences or merely the keeping of records. We are to discover the significancies to use in schemes of arrangement. . . . Marked variations which presumably have some constancy and are associated with geography or environment may be named and formally described in a taxonomic program, but study of variation itself is not a nomenclatorial problem, and the naming of inconstant or fugitive differences may obscure the undertaking. Taxonomy, or classification, stresses agreements.

Apart from the frequent assumptions of hybridity, and the former uncertainty connected with the identity of the holotypes, one of the other principal causes of confusion in the taxonomy of Amelanchier is the fact that specimens showing mere variations of foliage have been not infrequently described as new varieties or even species. Anyone who studies Amelanchier in the field, or who examines large series of specimens in herbaria, is at once struck by the extraordinary variation of the foliage that occurs even in the same species, as manifested in different stages of development and from various habitats. There is a great deal of difference between the appearance of specimens collected in the spring when the leaves are of thin texture and more or less pubescent, and specimens from the same shrub or tree in late summer or autumn when the leaves are larger, frequently somewhat coriaceous, and, with the exception of two western species, nearly or quite glabrous. The leaves of young shoots are usually much larger, and of diverse shapes and types of indentation. In the present paper no attempt has been made to describe these leaves; probably such descriptions would be either impossible or useless; instead, the descriptions have been drawn up from average normal leaves of the flowering and fruiting branches. For several of the species the following stages must be recognized and correlated before all specimens can be correctly identified: (1) specimens with unopened flowers and very young leaves, (2) specimens with opened flowers accompanied by half-unfolded leaves, (3) specimens from which the petals have

dropped, but with young unfolded leaves and young fruits, (4) specimens with mature leaves and fruits, (5) specimens with mature leaves but no fruits, and (6) specimens consisting only of leaves of vigorous young shoots. When placed side by side, specimens of the same species in these different stages of development often show an almost incredible dissimilarity and have been not infrequently mistaken for different species. However, collections of these different stages made over a period of years from the same plant, as from plants in cultivation in the Arnold Arboretum, and in the collections of feral plants made by critical field botanists, show conclusively that these extraordinary variations and "intergrades" are not at all, or only very rarely, due to hybridism, as has been frequently supposed, but are well within the range of normal variation of the species, not only among individuals in different habitats and other ecological conditions, but among different specimens from the same shrub or tree.

The taxonomic value of the kind of serration of the leaf-blades has to be estimated with caution. Nearly every species has a characteristic type of serration, but the range of variation within the species is frequently greater than that found between species. The statements, e.g., "leaves finely toothed," or "coarsely toothed," commonly used as key characters, may be often somewhat misleading, even though attempts are made to give them a semblance of quantitative value by recording the number of teeth per centimeter on average leaves, or the total number of teeth found on average blades. This is inevitable, because many species, including *A. spicata, A. florida,* and *A. pallida,* may have the blades finely toothed when young, while the mature leaves have a coarser indentation with fewer or larger teeth. It is only by confining the statement of indentation to the leaves of the flowering branches, or the fruiting branches, respectively, and then only by using the most general characterizations, that it is at all possible to use this character as a practical guide to the specific identity of the specimen under observation.

Similarly, over-emphasis must not be placed on the habit of the plant, which varies, of course, according to the habitat. Three American species —*A. arborea, A. interior,* and *A. laevis*—are arborescent, and under favorable conditions may become small or even moderate-sized trees, but under adverse conditions, shrubs many years of age may be only a foot or two in height. Certain other species, e.g., *A. spicata,* are usually dwarf, but under exceptionally favorable conditions may reach a height of two meters. However, it can be safely predicted that the truly frutescent species will never become trees, no matter how suitable the environmental conditions may be. In the western part of the continent especially, altitude is an important factor affecting the appearance of the plant, as is

also the wetness or dryness of the habitat. Certain species, e.g., *A. florida,* characteristically found at or near sea-level, may ascend the mountains to an altitude of 5000 feet or higher, where they show corresponding variations in their foliage, habit of growth, and general appearance. All these ecological variations must be taken into consideration in attempting to define the species.

In Amelanchier, as in most other genera of flowering plants, by far the most useful taxonomic characters are to be found in the morphological peculiarities of the flowers and fruits. The number of carpels, the length, and degree of fusion of the styles, the amount of pubescence of the top of the ovary, the number of stamens, the shape and size of the petals, and the shape, size, and direction of growth of the calyx-lobes, as well as the character of the inflorescence, are the best and most reliable structural criteria for taxonomic purposes.

Several explanations, including the theory of frequent hybridization previously mentioned, have been advanced from time to time to account for the peculiar variations within Amelanchier and related genera. However, certain available cytological data, although at present rather meager, seem to provide a more plausible alternative theory. The genera of the Pomoideae, including Amelanchier, that have been studied cytologically have been found to have a basic chromosome number of seventeen, or are polyploids with a basic number of seventeen. K. Sax (Journ. Arnold Arb. 12:3-21. 1931) reports that the pure species of Amelanchier that he studied are diploids, but two natural interspecific hybrids are tetraploids. In the same year, A. A. Moffett (Proc. Roy. Soc. Lond. ser. B, 108:423-446. 1931) investigated four species of Amelanchier and found that they are tetraploids. The chromosome number of the Pomoideae is a "secondary basic number (unbalanced relative to the primary basic number) and the derived series of polyploids ($2n = 34$, 51, 68) are secondary polyploids." As previously noted, the great variation within the genus Amelanchier often makes taxonomic study extremely difficult. "Such a condition is to be expected from a group of complex polyploids, whose polyploidy furnishes a mechanism for the segregation of numerous variations, but whose general character is evidently determined by their characteristic balance." It seems possible, therefore, that polyploidy may have played a more important part in the differentiation of genera and species in this subfamily than has heretofore been realized, since a change in chromosome balance is usually accompanied by a change in the morphological characters of the plant.

The following description of the wood of Amelanchier is taken from S. J. Record & R. W. Hess, *Timbers of the New World,* Yale University Press, 1943, pp. 447-448:

Heartwood brown or reddish brown, usually absent from small specimens; sapwood thick, slightly brownish; appearance of lumber usually marred by numerous brown lines (pith flecks). Luster medium. Odor and taste absent or not distinctive. Hard, heavy, compact, tough, and strong; sp. gr. (air-dry) 0.85; weight 53 lbs. per cu. ft.; texture fine and uniform; grain straight to irregular; rather easily worked, taking a good polish; dark heartwood durable. Of no commercial possibilities because of the scarcity and small size of the trees.

In the preparation of this paper, it has been necessary to study botanical material in several herbaria. For the loan of specimens, and for other courtesies, I wish to express my appreciation to the curators who have so generously placed the necessary specimens at my disposal. For assistance in the completion of this work I am particularly grateful to Dr. E. D. Merrill, Professor Alfred Rehder, and Dr. A. C. Smith, all of the Arnold Arboretum; to Dr. M. L. Fernald and Dr. L. B. Smith, of the Gray Herbarium; to Dr. J. M. Greenman, of the Missouri Botanical Garden; to Dr. F. W. Pennell and Mr. Bayard Long, of the Academy of Natural Sciences of Philadelphia; to Dr. H. A. Gleason and Mr. G. L. Wittrock, of the New York Botanical Garden; to Dr. Th. Just, of the University of Notre Dame, for the opportunity of examining material in the Greene Herbarium; to Dr. C. O. Rosendahl and Dr. E. C. Abbe, of the University of Minnesota; and to Dr. H. L. Mason, of the University of California, for a few specimens from Lower California. Thanks are due Dr. Leon Croizat of the Arnold Arboretum for nomenclatural and bibliographical assistance.

In the citation of specimens, the name of the herbarium to which the particular specimen belongs is indicated by the following standard abbreviations: (AA) Arnold Arboretum, (GH) Gray Herbarium, (NE) New England Botanical Club, (MBG) Missouri Botanical Garden, (UI) University of Illinois, (Ph) Academy of Natural Sciences of Philadelphia, (NY) New York Botanical Garden, (ND) University of Notre Dame, (Minn.) University of Minnesota, and (UC) University of California. Because of the large amount of material studied, it has been practicable to cite only part of the collections.

II. TAXONOMY

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Amelancher Bub. Fl. Pyren. 2:580 (1900).

TYPE SPECIES: *Mespilus Amelanchier* L. = *A. ovalis* Medic.

Slender often scaly-barked shrubs or small trees with unarmed branches and slender terete branchlets; wood hard, ring-porous; pith slightly 5-sided, pale, continuous; leaves simple, deciduous, alternate, petioled, pinnately veined, usually serrate or sometimes entire; leaf-scars narrowly crescent-shaped; bundle-traces 3; stipules linear, caducous, free from the petiole; stipule-scars lacking; winter-buds solitary, sessile, conspicuous, with several imbricate scales; flowers perfect, regular, entomophilous, in racemes (rarely solitary or paired) terminating short leafy branchlets of the season, appearing shortly in advance of the foliage, or as the leaves unfold; pedicels bracteate at the base and bearing a second bract at or near the middle; bracts scarious, pubescent, linear, deciduous about the time the flowers open; hypanthium campanulate or urceolate, more or less adnate to the carpels, becoming globose or ellipsoid in fruit;

disk nectariferous; calyx 5-lobed or 5-cleft, the lobes narrow, entire, imbricate in aestivation, persistent, becoming revolute or reflexed on the fruit, or sometimes remaining erect or ascending; petals 5, white, or rarely pink, oblanceolate to narrowly oval; stamens 10-20, short, inserted on the rim of the calyx; filaments subulate, more or less persistent on the fruit; styles 2-5, free or united at the base or to the middle; carpels 2-5, more or less united to form an inferior, compound, 2-5-loculed ovary, each locule 2-ovuled, but in fruit nearly divided by a false partition growing from the back of each carpel, thus forming an incompletely 4-10-loculed pome with one seed in each locule if all mature; carpel-walls of firm texture, not bony; pome small, mealy or juicy, berry-like, edible but often insipid; seeds small, smooth, dark brown; no endosperm.

Species and varieties of Amelanchier have been placed under a number of generic names, including Amelanchus, Amelancus, Aronia, Crataegus, Malus, Mespilus, and Pyrus, and have been transferred from one generic category to another. Amelanchier occupies a distinct position in the Pomoideae by its usually racemose inflorescence, distinctive foliage, and type of fruit with the peculiar carpels which have a false partition growing from the back of each. This latter character is also present only in the closely related monotypic genus Peraphyllum of western United States, and in Malacomeles of Mexico and Guatemala.

KEYS TO THE AMERICAN SPECIES

KEY TO FLOWERING SPECIMENS

1. Styles normally 5 (rarely 4); stamens 20; fruit becoming purplish black at maturity, glabrous, usually juicy and edible, mostly 10-loculed.
  2. Top of the ovary glabrous.
    3. Sepals more or less pubescent, at least on the ventral surface.
      4. Petals 3-9 mm. long; racemes erect; young leaves densely white-tomentose beneath; mature leaves elliptical or oval, serrulate acutish or obtuse and apiculate, the base rounded or acutish; Atlantic Coastal Plain.
        5. Racemes 2.5-6 cm. long, on leafy branchlets, the lower pedicels becoming 5-10 mm. long; petals oblanceolate; styles 4 mm. long, united beyond the middle; anthers 1 mm. long; fastigiately branched, alder-like shrubs, 3-8 m. tall, forming close bushy clumps; chiefly in swampy woods, moist thickets, or bogs.....................7. *A. canadensis*
        5. Racemes 1-3 cm. long, compact, leafless, the precocious flowers on very short pedicels only 1-3 mm. long; petals elliptical; styles 2-3 mm. loı , separate to below the middle; anthers 0.5-0.7 mm. long; low surculose colonial shrubs 0.2-1 m. high, forming loose colonies in open woods or sandy pine barrens................................8. *A. obovalis*
      4. Petals of the fully opened flowers 12-25 mm. long.
        6. Leaves short-acuminate at the apex, cordate or rounded at the base, usually ovate or obovate, finely serrate; racemes loose, becoming pendent or spreading, 4-12 cm. long; trees or tall shrubs of eastern North America.

       7. Leaves at flowering time about half-grown, nearly or quite glabrous, or only sparsely pubescent, bright green or bronze purple; sepals lanceolate, acuminate; racemes glabrous or nearly so; fruit sweet and juicy; lowest fruiting pedicels mostly 2.5-5 cm. long..5. *A. laevis*

       7. Leaves at flowering time scarcely unfolded, densely white-tomentose beneath; sepals oval-lanceolate, abruptly pointed; racemes sericeous; fruit somewhat dry, mealy and tasteless, falling early; lowest fruiting pedicels 1-2.5 cm. long............................6. *A. arborea*

    6. Leaves obtuse or acute at the apex, not acuminate; racemes erect or ascending, 2-5 cm. long; shrubs 1-3 m. tall; western North America.

       8. Petals 16-25 mm. long, 5-7 mm. wide above the middle; styles 3-4 mm. long; anthers 1-1.5 mm. long; leaf-blades thin, green, oval, 2.5-5 cm. long at maturity...........................14. *A. cusickii*

       8. Petals 12-16 mm. long, 3-4 mm. wide above the middle; styles 2-2.5 mm. long; anthers 0.8 mm. long; leaf-blades at maturity firm, pallid, suborbicular, 1.5-3 cm. long......................15. *A. basalticola*

3. Sepals, hypanthium, and pedicels perfectly glabrous, glaucous; whole plant perfectly glabrous; petals 8-12 mm. long; western United States.........

    ....16. *A. pumila*

2. Top of the ovary tomentose, usually densely so, rarely with only a few trichomes.

  9. Leaves permanently puberulent or finely tomentulose, at least on the lower surface; petals 5-11 mm. long; shrubs of western United States.

    10. Sepals lanceolate to deltoid-lanceolate; hypanthium and pedicels sparsely pubescent to glabrous; leaves with 7-9 pairs of lateral veins; second-year twigs usually brown and glabrous; top of hypanthium constricted on the fruit; California, southern Oregon and western Nevada....17. *A. pallida*

    10. Sepals linear or narrowly lanceolate to linear-spatulate; hypanthium and pedicels usually more or less densely lanate; leaves with 11-13 pairs of lateral veins; second-year twigs often puberulent, gray; hypanthium not at all or only slightly constricted on the fruit; Montana to New Mexico, westward to Lower California and eastern Oregon......18. *A. utahensis*

  9. Leaves at maturity glabrous or somewhat pubescent, never finely puberulent; the young leaves either glabrous or glabrescent (occasionally tardily so), or else densely floccose-tomentose, at least on the lower surface.

    11. Leaves usually more or less densely tomentose or floccose beneath at flowering time; shrubs or trees of the eastern half of North America. (Occasional specimens of the cordilleran *A. alnifolia* with tardily glabrescent leaves might also be sought here, as well as *A. arborea* var. *alabamensis*, whose flowers are unknown)

      12. Petals 4-10 mm. long; dwarf colonial shrubs 0.2-2 m. tall; leaves usually with 7-9 pairs of irregular lateral veins anastomosing near the usually rather finely serrate margins...............9. *A. spicata*

      12. Petals (of the fully opened flowers) 11-22 mm. long; shrubs (or small trees) 2-6 m. tall; leaves with 11-13 pairs of regular parallel conspicuous lateral veins, the uppermost extending into the teeth; margins coarsely serrate-dentate...................10. *A. sanguinea*

    11. Leaves not densely tomentose at flowering time, unfolded and more than half-grown, soon becoming nearly or quite glabrous on both surfaces.

      13. Leaves finely serrate, the teeth mostly 6-10 per cm., and 20-40 on each margin of average leaves of the flowering and fruiting branches.

        14. Flowers in 3-12-flowered racemes; petals oblanceolate, 8-13 mm. long; leaf-blades mostly rounded or slightly cordate at the base.

         15. Leaves usually elliptical or somewhat obovate, unfolded and more than half-grown and dull green and glabrous at flowering time, obtuse or acute at the apex, the base rounded; a

              low, stoloniferous, diffusely-branched shrub 0.3-1 m. tall; western Newfoundland, St. Paul I., the Magdalen Is., Anticosti I., and the coast of Quebec along the Gulf of St. Lawrence.....................................2. *A. fernaldii*

15. Leaves ovate or oval.

    16. Racemes 2-4 cm. long; leaves ovate, shortly acuminate, unfolded and more than half-grown and nearly or quite glabrous at flowering time; slender shrub 1-3 m. tall; Quebec to Massachusetts and Vermont, and adjacent New York.....................................3. *A. neglecta*

    16. Racemes loose, 4-7 cm. long; leaves oval, acute, unfolded but not fully grown at flowering time, the lower surface sparsely floccose-pubescent, varying to nearly or quite glabrous, sometimes the pubescence remaining until the petals have fallen; straggling or arching shrubs 2-3 m. tall, or small trees 7-8 m. tall; Minnesota, Wisconsin, and northern Michigan.........................4. *A. interior*

14. Flowers mostly in pairs or threes (or solitary), one terminal and the others in the axils of the upper leaves; blades glabrous, flat, oval, acute at each end; petals oval, 6-9 mm. long; a several-stemmed, loosely cespitose shrub 0.5-3 m. tall; Labrador and Newfoundland to the mountains of New England and New York to the Pocono Plateau, Pennsylvania, westward through Ontario to northern Michigan, and northwestern Minnesota..............
....1. *A. bartramiana*

13. Leaves more coarsely serrate, the teeth usually not more than 2-5 per cm., and only 5-20 on each margin of average blades.

17. Petals 6-10 mm. long, 2-3.5 mm. wide.

    18. Petals glabrous throughout; mature leaves relatively thin, the lower surface pale green; low shrubs 30-90 cm. tall; Gaspé Peninsula, Quebec, westward to the region about Lake Superior....................................11. *A. gaspensis*

    18. Petals pilosulous on the inside of the claw; mature leaves somewhat coriaceous, glaucous beneath; shrub or small tree 2-4 m. tall; Rocky Mountains and Great Plains of western North America..............................12. *A. alnifolia*

17. Petals 12-25 mm. long.

    19. Petals 12-15 mm. long (rarely shorter), 3-3.5 mm. wide; sepals deltoid-lanceolate, 2-2.5 mm. long; styles 2-2.5 mm. long; anthers 0.5-0.7 mm. long; summit of the ovary densely tomentose; Pacific Slope, from Alaska to northern California, west of the Cascade Mountains.................13. *A. florida*

    19. Petals 16-25 mm. long, 5-7 mm. wide; sepals lanceolate, acuminate, 3.5-5 mm. long; styles 3-4 mm. long; anthers 1-1.5 mm. long; summit of ovary nearly glabrous or with a ring of tomentum around the base of the styles; British Columbia to eastern Washington, eastern Oregon, Idaho, northern Utah, and western Montana.........14. *A. cusickii*

1. Styles 4, 3, or 2 (rarely 5); stamens 10-15 (-18); petals 5-10 mm. long; racemes erect or ascending, 2-4 cm. long; fruit usually small, 3-8-loculed, often drying brownish before maturity.

20. Petals oblanceolate.

    21. Leaves at maturity glabrous.

        22. Hypanthium sparsely pubescent outside at flowering time; western Washington and adjacent southern British Columbia................
....................................13a. *A. florida* var. *humptulipensis*

22. Hypanthium glabrous; southwestern United States and adjacent Mexico; glabrous forms of..............................18. *A. utahensis*
21. Leaves more or less puberulent or tomentulose, at least beneath; Rocky Mt. region, New Mexico to Montana, westward to eastern Oregon, southeastern California and adjacent Mexico...........18. *A. utahensis*
20. Petals oval or obovate; leaves puberulent (rarely glabrous); southwestern Oregon, California, and adjacent Nevada.....................17. *A. pallida*

KEY TO FRUITING SPECIMENS

1. Leaves glabrous at maturity, or rarely slightly pubescent beneath, never permanently puberulent.
   2. Styles normally 5; fruit glabrous and purplish black when ripe, usually juicy and edible, mostly 10-loculed.
      3. Top of the ovary tomentose, or tomentulose, rarely becoming nearly glabrous with age.
         4. Average leaves of the fruiting branches finely and sharply serrate or serrulate, the lanceolate teeth usually 5-10 per cm.; species occurring east of the 100th meridian.
            5. Style-base (as seen on the young fruit) thickened and tapering into the conical top of the densely tomentose ovary; styles on the young fruit 4-6 mm. long; sepals 3-4 mm. long, divaricate or reflexed, subulate-lanceolate; hypanthium more or less constricted below on the young fruit.
               6. Leaves oval or ovate, usually acute at each end, the petioles 4-12 mm. long; fruits solitary or in pairs or threes, or on robust specimens 4 or more in a somewhat corymbose raceme, ellipsoid-ovoid or somewhat pyriform, the larger 1-1.5 cm. in diameter when fully mature..1. *A. bartramiana*
               6. Leaves mostly elliptical or somewhat obovate, obtuse or acute at the apex, the base rounded; petioles 1-2.5 cm. long; fruits subglobose, 6-10 mm. in diameter at maturity, 5-10 in a slender raceme ....2. *A. fernaldii*
            5. Style-base not conspicuously thickened, the top of the ovary rounded or flattish; styles on the young fruit 2-3 mm. long; sepals reflexed or revolute, mostly oblong-lanceolate or triangular-lanceolate; leaf-base usually rounded or subcordate.
               7. Sepals 3-4 mm. long, reflexed; hypanthium not constricted on the young fruit.
                  8. Young leaves densely white-tomentose; tree 5-10 m. tall; mature leaves ovate or oval, acute or acuminate; Arkansas and Alabama ....6a. *A. arborea* var. *alabamensis*
                  8. Young leaves green and glabrous or nearly so from the first.
                     9. Leaves ovate, shortly acuminate; shrubs 1-3 m. tall; flowers in erect or ascending racemes 2-4 cm. long; Quebec to Massachusetts and Vermont, and adjacent New York..3. *A. neglecta*
                     9. Leaves oval, acute; straggling or arching shrubs 2-3 m. tall, or small trees 7-8 m. tall; flowers in nodding racemes 4-7 cm. long; Minnesota, Wisconsin, and northern Michigan........ ....4. *A. interior*
               7. Sepals 1.5-2.5 mm. long, usually revolute; hypanthium noticeably constricted on the young fruit; leaves commonly oval, acutish or obtuse, densely white-tomentose beneath when young; dwarf surculose colonial shrubs 0.2-2 m. tall.....................9. *A. spicata*
         4. Average leaves usually more coarsely toothed, the ovate teeth mostly 3-6 per cm.

10. Lower surface of mature leaves often pale green, but not glaucous; fruits 6-8 mm. in diameter at maturity; species occurring east of the 100th meridian.
    11. Tall straggling shrubs or small trees 2-6 m. tall; blades coarsely dentate-serrate, the lower surface, the petioles, and the rachis and pedicels of the young fruiting racemes often retaining traces of pubescence; lateral veins usually 11-13 pairs, conspicuous, parallel, the upper ones ending in the teeth; styles on the young fruit mostly 3-5 mm. long.........................10. *A. sanguinea*
    11. Low shrubs 0.3-2 m. tall; principal lateral veins of the leaves fewer and less regular; styles on the young fruit 2-3 mm. long.
        12. Principal lateral leaf-veins mostly 9-11 pairs, the upper ones usually extending to the margin and ending in the teeth, the others anastomosing at their tips; racemes and mature leaves quite glabrous; low, much-branched shrubs 30-90 cm. tall, often forming dense thickets; Gaspé Peninsula, Quebec, westward to the region about Lake Superior.....11. *A. gaspensis*
        12. Principal lateral veins mostly 7-9 pairs, somewhat irregularly and distantly arranged, usually anastomosing before reaching the margin; racemes, petioles, and lower part of underside of blades often retaining traces of grayish tomentum; low stoloniferous colonial shrubs 0.2-2 m. tall; Newfoundland to eastern North Dakota, southward to Missouri and Georgia ....9. *A. spicata*
  10. Lower surface of leaves usually glaucous; the margins ordinarily rather coarsely toothed, chiefly on the upper half of the usually obtuse blade; fully developed fruits normally 1-1.5 cm. in diameter; shrubs 2-4 m. tall, or small trees, of western North America.
    13. Mature blades usually more or less suborbicular, subcoriaceous; petals 6-10 mm. long; species of the Rocky Mountains and Great Plains..12. *A. alnifolia*
    13. Mature blades frequently oval and of thinner texture; petals 12-15 mm. long; species of the Pacific Slope, Alaska to northern California, west of the Cascade Mountains.........13. *A. florida*
3. Top of the ovary glabrous, rarely with a few trichomes.
  14. Leaves finely and sharply serrate or serrulate almost to the base of the blade, the teeth usually 6-11 per cm., 20-60 on each side of average blades; eastern North America.
    15. Low colonial surculose shrubs 0.2-1.5 m. tall; fruiting pedicels mostly 3-8 mm. in length; sepals on the fruit usually erect or divaricate...8. *A. obovalis*
    15. Tall shrubs or small trees; lower fruiting pedicels becoming 1-5 cm. long.
        16. Sepals on the fruit usually erect or ascending, rarely somewhat reflexed; fruiting racemes erect, compact, the lower pedicels 1-2 cm. long; leaves usually elliptical, varying to narrowly obovate, oblanceolate, or oval, the apex acute, or obtuse and mucronate; shrubs 2-8 m. tall, somewhat fastigiately branched; chiefly Atlantic Coastal Plain........................7. *A. canadensis*
        16. Sepals on the fruit reflexed or recurved, rarely remaining erect or divaricate; fruiting racemes loose, the lower pedicels longer; leaves ovate or oval, short-acuminate or acute at the apex, the base cordate or rounded; small trees 10-20 m. tall, or tall shrubs, with ascending or spreading branches.

      17. Sepals lanceolate to subulate, acuminate, 3-4.5 mm. long on
the fruit; lowest fruiting pedicels mostly 2.5-5 cm. long;
blades, and usually the petioles, completely glabrous; fruit
sweet and succulent.............................5. *A. laevis*

      17. Sepals triangular-lanceolate or oblong-lanceolate, abruptly
pointed, 2-3 mm..long on the fruit; lowest pedicels 1-2.5 cm.
long; petioles, and often the underside of the blades (at least
near the base), frequently retaining some pubescence at ma-
turity; fruit somewhat dry, mealy, insipid......6. *A. arborea*

  14. Leaves more coarsely serrate, the teeth 3-6 per cm., 3-15 on each side of
average blades; apex obtuse or acutish; winter buds conical, acute;
shrubs 1-3 m. tall; western North America.

    18. Sepals more or less pubescent within.

      19. Sepals deltoid, 3-3.5 mm. long; petals 16-25 mm. long; leaves
thin, green, mostly 2.5-5 cm. long, mostly oval....14. *A. cusickii*

      19. Sepals linear-lanceolate, 4-5 mm. long; petals 12-16 mm. long;
leaves at maturity firmer, pallid, suborbicular, 1.5-3 cm. long
....15. *A. basalticola*

    18. Sepals, hypanthia, and pedicels perfectly glabrous, glaucous; whole
plant perfectly glabrous; petals 8-12 mm. long........16. *A. pumila*

2. Styles 3 or 4; petals 6-10 mm. long.

    20. Calyx and ovary pubescent; western Washington and southern Vancouver
Island................................12a. *A. florida* var. *humptulipensis*

    20. Calyx and ovary glabrous; Nevada and Arizona; glabrous forms of....
....18. *A. utahensis*

1. Leaves usually permanently puberulent or tomentulose, at least beneath, varying
to cinereous (rarely glabrous); petioles pubescent (except shade forms); styles
usually 4, 3, or 2 (rarely 5); fruit usually small, 3-6-loculed, often sparsely
pubescent at first, frequently drying brownish before maturity; shrubs of western
United States and Lower California.

    20. Hypanthium more or less constricted on the young fruit; sepals lanceolate to
deltoid-lanceolate; styles 4 or 3 (rarely 5), united below; leaves entire to ser-
rate, usually with 7-9 pairs of lateral veins; southwestern Oregon, California,
and adjacent Nevada...17. *A. pallida*

    20. Hypanthium not at all constricted on the fruit; sepals subulate-lanceolate to
linear-spatulate; styles 2, 3, or 4, free nearly to the base; leaves usually
coarsely toothed, varying to nearly entire, usually strongly reticulate and with
9-13 pairs of lateral veins; Rocky Mountain region, New Mexico to Montana,·
westward to eastern Oregon and Lower California..........18. *A. utahensis*

III. DESCRIPTION AND DISCUSSION OF SPECIES

1. AMELANCHIER BARTRAMIANA (Tausch) M. Roemer

(Plates I and XI)

Mespilus canadensis var. δ *oligocarpa* Michx. Fl. Bor. Am. 1:291 (1803).
Pyrus oligocarpa nana Donn ex Muhlenberg, Cat. Pl. Am. Sept. 49 (1813).
Pyrus bartramiana Tausch in Flora 21:715 (1838).
Aronia praecox Neumann ex Tausch, l.c., pro syn.
Amelanchier canadensis var. ε *oligocarpa* Torrey & Gray, Fl. N. Am. 1:474 (1840);
 Torrey, Fl. N.Y. 1:226 (1843); Walpers, Rep. Bot. Syst. 2:55 (1843); Gray,
 Man. 131 (1848); Farwell in Rep. Mich. Acad. Sci. 17:175 (1916).
Amelanchier bartramiana M. Roem. Syn. Mon. 3:145 (1847); Wiegand in Rhodora
 14:158, pl. 96 (1912); Britton & Brown, Illustr. Fl. N. U.S. (ed. 2) 2:293, fig.
 2334 (1913); Rehder in Bailey, Stand. Cyclop. Hort. 273, fig. 188 (1914); Hoff-
 mann in Proc. Boston Soc. Nat. Hist. 36:280 (1922); Pease in ibid. 37:267
 (1924); Rehder, Man. Cult. Tr. & Shr. 390 (1927); Rydberg, Fl. Prairies &
 Plains 438 (1932); Marie-Victorin, Fl. Laurent. 317, fig. 91 (1935); Nielsen
 in Am. Midl. Nat. 22:189, pl. 15 (1939); Rehder, Man. Cult. Tr. & Shr. (ed. 2)
 389 (1940).
Amelanchier oligocarpa M. Roem. Syn. Mon. 3:145 (1847); Watson & Coulter in
 Gray, Man. Bot. (ed. 6) 167 (1889); Dippel, Handb. Laubh. 3:391, fig. 196
 (1893); Britton & Brown, Illustr. Fl. N. U.S. 2:239, fig. 1990 (1897); Keeler,
 Our Northern Shr. 196 (1903); Schneider, Illustr. Handb. Laubh. 1:737, figs.
 411, 412 (1906); Britton, Man. N. States 518 (1901), (ed. 3) 518 (1907); Card
 in Bailey, Cyclop. Am. Hort. 57 (1904); Robinson & Fernald in Gray, New
 Man. Bot. (ed. 7) 460 (1908); Jones & Rand in Bull. Vermont Agr. Exp. Sta.
 145:101 (1909); Apgar, Ornam. Shr. U.S. 182, fig. 280 (1910); Clements,
 Rosendahl, & Butters, Minnesota Tr. & Shr. 153 (1912); Bean, Tr. & Shr.
 Brit. Isles 1:189 (1914).
Amelanchier sanguinea sensu Decaisne in Nouv. Arch. Mus. Hist. Paris 10:136
 (1874). Non *A. sanguinea* (Pursh) DC.
Amelanchier arguta Nuttall ex Britton, Man. N. States (ed. 2) 1066 (1905), (ed. 3)
 1076 (1907).
Amelanchier canadensis var. *pauciflora* Farwell in Rep. Mich. Acad. Sci. 17:175
 (1916).

A several-stemmed loosely cespitose shrub 0.5-3 m. tall; stems ascend-
ing, slender; bark grayish brown; twigs slender, glabrous, brown, with
small oval lenticels; winter buds small, brown, lanceoloid, acuminate, the
scales glabrate except the ciliolate margins; leaves flat and imbricate in
the bud, glabrous from the first, about half-grown at flowering time, firm
and pale green and slightly glaucous beneath at maturity; blades of the
flowering and fruiting branches oval, varying to elliptical, obovate, or sub-
orbicular, 3-6 cm. long, 1.5-4 cm. wide, usually acutish at each end, or the
base cuneate, less commonly somewhat rounded; principal lateral veins
10-16 pairs, not prominent, irregularly spaced, curved upward, forking
and anastomosing near the margin, often with shorter intermediate ones;
margins finely and sharply serrate or serrulate or sometimes double-
serrate to below the middle or near the base of the blade, the teeth
obliquely acuminate, 6-10 per cm., 20-40 on each margin; stipules cadu-
cous, linear, sericeous, about 1 cm. long; petioles usually short, glabrous

or sparingly ciliolate, those of the leaves of the fruiting branches mostly 4-12 mm. long; flowers solitary or few together, one terminal, the others in the axils of the upper leaves, the pedicels slender, glabrous, 1-3 cm. long; petals white, oval, obtuse, widest near the middle, 6-9 mm. long; stamens longer than the styles; filaments glabrous; anthers 1 mm. long, sepals lanceolate, acuminate, glabrous outside, tomentulose within; fruits solitary or in pairs or threes, or on robust specimens 4-6 in a somewhat corymbose raceme, but usually only one or two of them developing to full size at maturity; hypanthium more or less constricted on the young fruit; sepals on the fruit varying from nearly erect to divaricate or reflexed, (3-) 4-5 mm. long, glabrous outside, tomentulose within, lanceolate-subulate; styles 5 (or 4), united below the middle, 4-5 mm. long, tomentose at the base; ovary densely tomentose, tapering into the somewhat thickened style-base; mature fruits ellipsoid-ovoid or somewhat pyriform, glabrous, dark purple, glaucous, edible but insipid, ripening in July or August, the larger ones 1-1.5 cm. in diameter; pedicels glabrous, 1-3 cm. long; seeds few, or only 1 maturing, dark brown, smooth, glabrous, asymmetrically ovoid or lanceoloid, 3.5-4.5 mm. long, 2-3 mm. thick.

TYPE LOCALITY: [Northeastern] North America. Isotype in the herbarium of the Missouri Botanical Garden. Phototype in the herbarium of the Arnold Arboretum of Harvard University.

RANGE: Mountain woods, cold swamps and bogs, or in wet rocky soil, often at medium or higher altitudes, from Labrador and Newfoundland to the mountains of New England and New York, to the Pocono Plateau, Pennsylvania, westward through Ontario to northern Michigan and northeastern Minnesota. Flowering from May 15 to June 10; fruit ripe in July and August.

LABRADOR: Caribou I. in 1860, *Chapin* (UI); Petty Harbour, *Bishop* 371 (GH, AA), Hopedale, *Bishop* 370 (GH, AA); Makkovik, *Stecker* 19 (GH); Red Bay, *Sandborger* 20 (GH); Betchewan, *Abbe* 1136 (GH).

QUEBEC: East Main, east coast of James Bay, *Potter* 487 (GH); Mt. Sherrick, *Potter* 486 (GH); L. Mistassini, Aug. 12, 1885, *Macoun* (GH); Orford, Sherbrooke Co., *Pease* 11969 (GH); St. Agathe des Monts, June 1, 1903, Aug. 26, 1902, *Jack* (AA); Brion I., Magdalen Islands, *St. John* 1903 (GH); Thetford, Megantic Co., *M.-Victorin* 11214 (AA); Black Lake, Megantic Co., *Fernald & Jackson* 10107 (GH); Lac Saint-Jean, *M.-Victorin* 15589 (AA); St. Pierre, *Arsène* 311 (GH); Anticosti I., *M.-Victorin & Rolland-Germain* 27901 (GH), 27899 (GH, AA); Matamek River, *Bowman* 26, 237, 402 (GH); Rimouski Co., *Collins & Fernald* in 1904 (GH), *Fernald & Collins* 1100 (GH), *Rousseau* 26228 (GH, AA), 26771 (AA); Harrington, *Abbe* 1151 (GH); Saguenay Co., *St. John* 90526, 90527, 90528, 90529 (GH), *Robinson* 782 (GH), July 14, 1892, *Kennedy* (GH); Sept-Iles, Gaspé Co., *M.-Victorin & Rolland-Germain* 18707, 18708, 18709 (GH); Mt. Albert, *Collins & Fernald* in 1905 (GH), *Fernald & Collins* 233 (GH), *M.-Victorin, et al.* 17436 (GH, AA); Table Top Mt., *Fernald & Collins* 614 (GH), *Rousseau & Fortier* 31441, *M.-Victorin, Rolland-Germain, & Jacques* 33486, 33467 (GH); Montagne Ste.-Anne, *M.-Victorin, et al.* 17433 (GH, AA).
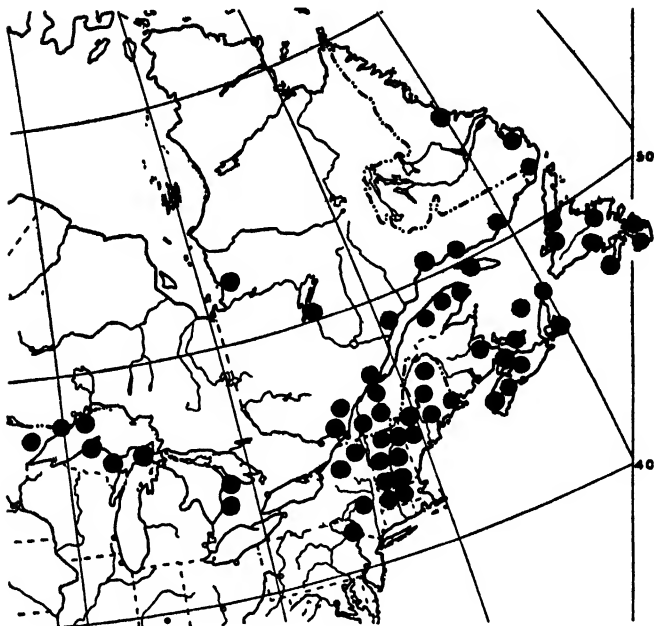
MAP 1.—Range of *Amelanchier bartramiana.*

NEWFOUNDLAND: Avalon Bay, *Fernald & Wiegand* 5574, 5574a, 5576, 5578, 5755 (GH); Valley of Exploits River, *Fernald & Wiegand* 5597, 5600, 5602, 5736, 5737, 5739, 5742, 5743, 5744, 5749, 5751, 5752, 5754 (GH), 5738 (GH, AA); Conception Bay, *Howe & Lang* 1203 (GH); St. John Bay, *Fernald, Long, & Fogg* 1789 (GH); Spruce Brook, *Kennedy* 17 (GH); Crabbes Station, *Kennedy* 257 (GH); Notre Dame Bay, *Fernald & Wiegand* 5535, 5745, 5746, 5756 (GH); Bay of Islands, *Fernald, Long, & Fogg* 292 (GH), *Fernald & Wiegand* 3554, 5748, 5750 (GH), *Mackenzie & Griscom* 10327 (GH), *Howe & Lang* 1081 (GH); Bonne Bay, *Kimball* 102 (GH); Hermitage Bay, *W. Palmer* 1340 (GH).

NEW BRUNSWICK: Bass River, June 1, 1871, July 2, 1875, *Fowler* (GH); Serpentine River, *Hay* 63 (GH); Kent Co., May 29, 1868, *Fowler* (GH).

NOVA SCOTIA: Ohio, *Jack* 3106 (GH); Weymouth, *Jack* 3344 (GH); Folleigh, *Bean, White, & Linder* 21459 (GH, AA); St. Paul I., *Perry & Roscoe* 244 (GH).

PRINCE EDWARD ISLAND: Queens Co., *Fernald, Long, & St. John* 7596, 7597 (GH).

MAINE: Mt. Katahdin, July 1900, *Fernald* (GH, NE); Somerset Co., Aug. 18, 1896, *Fernald* (NE), *Fernald & Pease* 25133 (NE), *St. John & Nichols* 2332 (NE); Franklin Co., *Furbish* in 1894 (NE), *Chamberlain & Knowlton* in 1902 (NE); Orono, May 14, 1892, *Fernald* (NE); Penobscot Co., *Fernald* in 1897 (NE); Marshfield, Aug. 2, 1916, *Knowlton* (NE); Greenville, *Fernald* 257 (GH, NE); Winn, *Fernald & Long* 13782 (NE); South Poland, *Furbish* in 1893 (NE); Fort Kent, *Fernald* 2314 (GH, NE).

NEW HAMPSHIRE: "White Mts., N. Hampshire," *Nuttall* (type coll. of *A. arguta*) (GH); Crawford Mill Pond, June 4, 1881, *Faxon* (GH, NE); Jaffrey, *Rand & Robinson* 616 (GH); Mt. Moosilanke, July 12, 1886, *Faxon* (GH); May 11, 1895, *Churchill* (GH, NE); Franconia, May 31, 1892, *Faxon* (GH, NE), *Fernald & Smiley* 11720 (NE); Tuckerman's Ravine, *Sargent* in 1879 (AA), *Eggleston* 2369 (GH, UI), July 6, 1888, *Faxon* (GH, NE), July 17, 1891, *Kennedy*

(NE); Mt. Washington, *Greenman* 1058 (GH, MBG), July 12, 1855, *Wm. Boott* (NE); Mt. Ingalls, *Pease* 11205 (NE); Whitefield, *Pease* 16683 (NE, UI); Mt. Madison, *Pease* 10216 (NE); Carter Notch, *Pease* 4090 (NE); Carroll, *Pease* 14372 (NE); Stewartstown, *Pease* 16662 (NE); Sugarloaf Mt., *Pease* 13482 (NE); Berlin, *Pease* 25275 (NE); Pittsburg, *Pease* 10312 (NE).

VERMONT: Mt. Mansfield, July 3, 1897, *Williams* (GH, NE), *Churchill,* July 5, 1897 (NE), *Greenman* 936 (MBG), *Pringle* in 1878 (AA), *Eggleston* in 1893 (GH); Willoughby, July 8, 1898, *Kennedy* (NE); Woodford, June 20, 1925, *Carpenter, Churchill, & Knowlton* (NE); Mt. Killington, June 18, 1899, *Eggleston* (NE, UI), May 1913, *Dutton* (GH, NE); Rutland, *Eggleston* 1960, 1964 (GH, NE); Barton, May 24, 1923, *Knowlton* (NE); Coventry, May 19, 1932, *Knowlton* (NE); Craftsbury, May 19, 1932, Knowlton (NE); Greensboro, May 18, 1938, *Knowlton* (NE); Lowell, May 23, 1935, *Knowlton* (NE); Lunenburg, July 9, 1915, *Woodward* (NE); Sutton, May 20, 1932, May 18, 1933, *Knowlton* (NE); Searsburg, *Pease* 19561 (NE); Stratton, *Eggleston* 1962 (GH), *Blanchard* 5 (GH, AA).

MASSACHUSETTS: Mt. Greylock, June 2, 1901, *Churchill* (GH, NE), June 16, 1901, *Williams* (GH), June 25, 1916, *Hoffmann* (NE), *G. N. & F. F. Jones* 16170 (UI); Florida, July 3, 1909, July 14, 1916, *Hoffmann* (NE); Hubbardston, *Weatherby, Smith, et al.,* Pl. Exsicc. Gray. 959 (GH, UI); Ashburnham, May 19, 1924, *Knowlton* (NE).

NEW YORK: Canton, *Phelps* 1588, 1589 (GH); Essex Co., *House* 7264, 9468, 10227 (GH); Tug Hill Plateau, *Hotchkiss* 2290 (GH); Mt. McIntyre, *Muenscher & Clausen* 4020 (GH).

PENNSYLVANIA: Pocono Mts., July 27, 1893, *Porter* (GH).

ONTARIO: Wingham, *Morton* 2691 (UI); Long Lake, *Jennings* 14015 (GH); Sandy Inlet, *Krotkov* 5384 (GH).

MICHIGAN: Keweenaw Peninsula, *Farwell* 52d (GH), *Fernald & Pease* 3360 (GH); *Gwinn,* June 6, 1909, *Harrison* (GH); Isle Royale, *Cooper* 46 (GH).

MINNESOTA: Vermilion Lake, *Arthur, Bailey, & Holway* B407 (GH).

An examination of a part of the type collection from the Bernhardi Herbarium, now in the Missouri Botanical Garden, leaves no doubt of the identity of this species, or that it is the same as Michaux's *Mespilus canadensis* var. δ *oligocarpa,* as shown by a comparison of phototypes in the Gray Herbarium and the Arnold Arboretum.

Amelanchier bartramiana is usually to be distinguished by the small flowers occurring mostly in pairs or threes or solitary, one terminal and the others in the axils of the upper leaves, which are oval, acute at each end, short-petioled, finely serrate, and quite glabrous from the first. The styles on the young fruits are thickened at the base and taper into the conical top of the densely tomentose ovary. It has been usually assumed that the number of flowers and fruits never exceeds 1-3, or 4, and that occasional robust specimens bearing a larger number in a somewhat corymbose inflorescence must belong to plants of hybrid origin that have resulted from crosses with either *A. laevis* or *A. spicata.* That this need not necessarily be the case is shown by certain specimens that evidently possess all the other diagnostic characters usually attributed to *A. bartramiana.* It may be pointed out, however, that when the number of fruits exceeds two or three, usually only the terminal ones attain full size at maturity, the others remaining small and failing to develop.

Amelanchier arguta Nuttall ex Britton, published in 1905 without citation of a type or any definite reference to the source of the name, does not differ in any essential respect from *A. bartramiana* (Tausch) M. Roem. One of Nuttall's specimens, from "White Mts., N. Hampshire, also on Wachusett Mt., Mass.," has been examined in the Gray Herbarium.

A specimen (*Weatherby, Smith, & Rollins* 6909) collected near Hubbardston, Worcester County, Massachusetts, on May 23, 1939, appears to be a hybrid between *A. bartramiana* and *A. canadensis*. The collection data on the label of the specimen are: "Low, loosely cespitose shrub in bushy flats. With parents, flowering later than *A. bartramiana*."

2. AMELANCHIER FERNALDII Wieg.
(Plates I and IV)

Amelanchier fernaldii Wiegand in Rhodora 22:149 (1920).

Low surculose, straggling, diffusely branched shrubs 0.3-1 m. tall, growing in colonies or large clumps; bark of the branches gray or brown, smooth; twigs glabrous; winter buds small, conical, acute, glabrous or nearly so; leaves conduplicate in the bud, unfolded and more than half-grown, dull green and glabrous at flowering time, of rather thin texture; mature blades firm, elliptical or somewhat obovate, glabrous on both sides, paler beneath, darker green and often somewhat impressed-veined above, 5-8 cm. long, 1.5-4.5 cm. wide, the apex obtuse or acute, the base rounded; lateral veins irregular, 7-13 pairs; margins sharply serrate from near the base, the acuminate teeth 4-10 per cm., 15-35 on each side of average leaves of the flowering and fruiting branches; stipules linear, caducous, 0.5-1 cm. long, 0.5-1 mm. wide, glabrous or pubescent; petioles slender, glabrous or sparsely pilose, 1-2.5 cm. long on average leaves; flowers small, in erect or ascending, loose, 3-8-flowered racemes 2-4 cm. long; rachis and pedicels glabrous; petals 5, white, glabrous, oval or oblanceolate, obtuse, 8-11 mm. long, 5-6 mm. wide; stamens 20, the filaments glabrous, 2-4 mm. long; anthers 1 mm. long; hypanthium campanulate, 4-5 mm. in diameter, glabrous; sepals linear-lanceolate, acuminate, tomentulose within, glabrous outside, 3-5 mm. long, erect or soon irregularly divaricate; styles 5, glabrous, united near the base, 3-4 mm. long; summit of the ovary densely tomentose; mature fruits 6-10 mm. in diameter, 10-loculed, glabrous, purplish black and juicy at maturity; pedicels 3-4 cm. long; seeds brown, smooth, obliquely lanceloid, acute at each end, 4-5 mm. long, 2-2.5 mm. wide. ,

TYPE LOCALITY: Grindstone, Grindstone Island, Magdalen Islands, Quebec, Canada. Type in the Gray Herbarium of Harvard University.

RANGE: In wet woods and thickets, borders of swamps, "lime barrens or strongly calcareous shores and swamps" (Wiegand, l.c.), or damp hollows in sand dunes, western Newfoundland, St. Paul Island, the Magdalen Islands, Anticosti Island, and the coast of Quebec along the Gulf of St. Lawrence. Flowering from the end of June to the latter part of July; fruit ripening in July and August.

NEWFOUNDLAND: Table Mt., Port au Port Bay, *Fernald & St. John* 10840, 10841 (GH), 10842 (GH, AA); Old Port au Choix, St. John Bay, *Fernald, Long, & Fogg* 1792 (GH).

NOVA SCOTIA: St. Paul Island: Ethel Lake, *Perry & Roscoe* 243 (GH).

PRINCE EDWARD ISLAND: Bothwell, *Fernald & St. John* 11083 (AA).

QUEBEC: Magdalen Islands: Grindstone Island, *Fernald, Long, & St. John* 7592 (GH, TYPE), 7590 (GH), *Fernald, Bartram, Long, & St. John* 7586 (GH), 7589 (AA, GH); Coffin Island, *Fernald, Bartram, Long, & St. John* 7587 (GH); Brion Island, *St. John* 1909 (GH); Anticosti Island, *M.-Victorin & R.-Germain* 27898 (GH); Riviere Vaureal, *M.-Victorin & R.-Germain* 27900 (GH); Grand River, Gaspé Co., *Fernald* in 1904 (GH); Cap Original, *M.-Victorin, R.-Germain, & Jacques* 33216 (GH); Sept-Iles, *M.-Victorin & R.-Germain* 18710, 18711 (GH); Isle-aux-Coudres, *M.-Victorin* 4318 (AA, GH); Grand Barachois, *M.-Victorin & R.-Germain* 9507 (GH, AA); Anse Pleureuse, *M.-Victorin, R.-Germain, & E. Jacques* 33436, 33439 (GH).

Although *A. fernaldii* has some characteristics suggesting a hybrid origin, it "seems to form a definite unit, not a fluctuating hybrid" (Wiegand, l.c.), and may be regarded as a small endemic species of the region about the Gulf of St. Lawrence. From *A. bartramiana* it is to be distinguished by its racemose inflorescence, elliptical leaves with longer petioles, and longer petals and smaller fruits.

The leaves of *A. fernaldii* are the same general shape as those of *A. canadensis*, but there is little likelihood of the two species being confused. The leaves of the former are glabrous, flat, and often nearly full-grown at flowering time, while those of the latter are folded, less than half-grown, and densely whitish tomentose. Also, the flowers of *A. fernaldii*, with their woolly-topped ovaries, and their longer sepals, are in nearly glabrous, looser racemes.

3. AMELANCHIER NEGLECTA Egglest.

(Plates I and V)

Amelanchier neglecta Eggleston, in herb.

Slender-stemmed, shrubs 1-3 m. tall, with grayish brown bark and glabrous twigs; winter buds small, glabrous, conical; leaves conduplicate in the bud, unfolded and more than half-grown and nearly or quite glabrous at flowering time; mature blades ovate or oval, glabrous throughout, paler beneath, of firm texture, 5-6 cm. long, 2-3 cm. wide, the apex usually shortly acuminate, the base rounded or subcordate; lateral veins

7-11, curved, anastomosing toward the edge of the leaf; margins finely and sharply serrate nearly to the base, the teeth 7-9 per cm., 20-30 on each margin of average leaves of flowering and fruiting branches; stipules linear, fugacious, slightly pubescent; petioles of mature leaves 1-2 cm. long, glabrous; flowers small, in erect or ascending 7-10-flowered racemes 2-4 cm. long; rachis and pedicels glabrous; petals 5, white, glabrous, narrowly oval, mostly 8-10 mm. long, about 4 mm. wide; stamens 20, the filaments glabrous, 2-3 mm. long; anthers 1 mm. long; hypanthium campanulate, 3-4 mm. in diameter, glabrous; sepals linear-lanceolate, acuminate, tomentulose within, glabrous outside, 3-4 mm. long, soon recurved or reflexed; styles 5, glabrous, united near the base, 3-4 mm. long; summit of the ovary densely tomentose; mature fruits 8-10 mm. in diameter, subglobose, 10-loculed, glabrous, purplish black and juicy at maturity; pedicels 15-25 mm. long; seeds smooth, brown, asymmetrical, obliquely lanceoloid, acute at each end, 4-5 mm. long.

TYPE LOCALITY: Rutland, Vermont. Collected by W. W. Eggleston in 1899. Type in the Gray Herbarium of Harvard University.

RANGE: Growing at the edge of clearings, in damp thickets and open woods that have been recently burned, or on ledges and talus, or in mossy spruce barrens, southern Quebec, Prince Edward Island and Nova Scotia to Massachusetts, Vermont, and adjacent New York. Flowering in May and June; fruits ripening in July and August.

QUEBEC: Gaspé Bay, Aug. 23, 1897, *Jack* (AA); Montmagny, *Rousseau* 24557 (AA, GH); Lac Long, *Rousseau* 24552 (GH); Montmorency Falls, *Macoun* 66927 (GH); Ottawa River, *Bro. Rolland* 7214 (GH).

NEW BRUNSWICK: Woodstock, *Fernald & Long* 13764 (GH).

NOVA SCOTIA: Meteghan, *Fernald & Long* 21450 (GH).

PRINCE EDWARD ISLAND: Charlottetown, *Fernald & St. John* 7578 (GH); Mt. Stewart, *Fernald, Bartram, Long, & St. John* 7581 (GH).

MAINE: Fort Fairfield, *Fernald* 37 (NE); Northport, *Furbish* in 1891 (NE); Brownville, *Parlin* 1811 (GH); East Livermore, *Furbish* in 1878 (NE); Dover, June 29, 1894, *Fernald* (NE); Fort Kent, *Fernald* 2312 (GH, NE); Oxford, *Chamberlain* in 1907 (NE); Moxie Mt., Aug. 25, 1902, *Collins & Chamberlain* (NE); Cutler, July 7, 1902, *Kennedy, et al.* (GH); Mt. Katahdin, July 17, 1900, *Churchill*
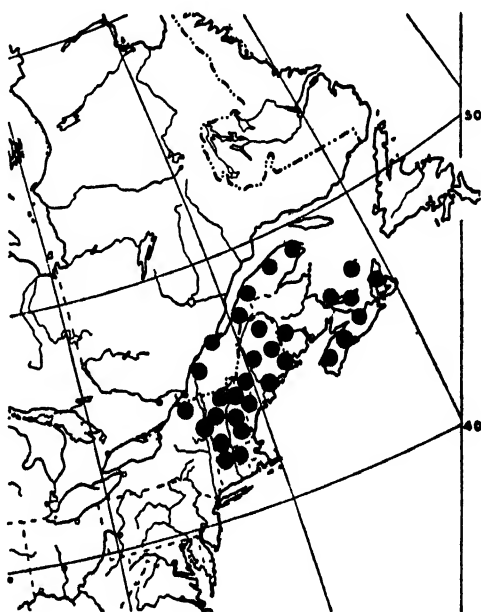
MAP 2.—Range of *Amelanchier neglecta*.

(NE); Isle au Haut, *Hill* 1614 (NE); Orono, *Fernald,* July 6, 1892, *Furbish* in 1891 (NE); Winn, *Fernald & Long* 13768, 13769 (NE); City Camp, July 17, 1900, *Fernald* (AA, NE, GH); Jonesboro, Aug. 1, 1932, *Knowlton* (NE); Roque Bluffs, July 11, 1908, *Knowlton* (NE).

NEW HAMPSHIRE: Flume, *Sargent* in 1879 (AA); Gorham, *Cusick* in 1887 (GH); Randolph, *Moore* 4189 (GH), *Pease* 670 (NE); Crawford House, June 6, 1881, *Faxon* (GH); Franconia, June 26, 1895, *Faxon* (GH); Colebrook, *Fernald & Pease* 16825 (NE); Carroll, *Pease* 14374 (NE); Pittsburg, *Pease* 10995 (NE); Shelburne, July 12, 1882, *Deane* (NE); Baldface Mt., *Pease* 16044 (NE); Stewartstown, July 19, 1917, *Fernald & Pease* (NE); Gilmanton, *Cushman & Sanford* 1217 (NE); Gilford, *Harris & Pease* 26551 (NE); New Hampton, *Pease* 26527 (NE); Plymouth, *Fernald* 11719 (NE); Mt. Agassiz, July 1871, *Collins* (NE).

VERMONT: Manchester, *Day* 379 (GH, NE); Johnson, *Grout,* June 8, 1895 (NE); Willoughby, May 26, 1904, May 19, 1905, *Kennedy* (NE); Orange, May 17, 1932, *Knowlton* (NE); Sutton, May 20, 1932, *Knowlton* (NE); Brandon, May 26, 1912, *Knowlton* (NE); Rutland, *Eggleston* 1118, 1173, 1174, 1175, May 12, June 21, July 7, 1899 (TYPE coll., GH, NE).

MASSACHUSETTS: Westminster, May 10, 1912, *Hunnewell & Wiegand* (NE); Hanging Mt., July 12, 1906, *Hoffmann* (NE); Lanesboro, May 19, 1920, *Hoffmann* (NE); Florida, June 5, 1920, July 14, 1916, *Hoffmann* (NE); Sheffield, May 24, 1920, *Hoffmann* (NE).

NEW YORK: Black Lake, St. Lawrence Co., *Muenscher & Maguire* 2319 (GH), 2320 (MBG); Washington Co., *Burnham* 21 (GH); Newcomb, *House* 10189 (GH).

Amelanchier neglecta has often been regarded as a natural hybrid between *A. bartramiana* and *A. laevis* because in several respects it appears to be somewhat intermediate between these two species. It resembles *A. laevis* in the conduplicate vernation of the finely toothed, usually acute, or shortly acuminate leaves that are quite glabrous, even at flowering time. It is, however, of smaller stature than *A. laevis,* and differs in the constantly tomentose ovary, shorter petals, and longer styles. It also shows some resemblance to *A. bartramiana,* but differs in the habit of growth, and in the smaller, usually more numerous, constantly racemose flowers and fruits. The usually ovate, short-acuminate leaves, which are rounded or cordate at the base, are of different color and texture, and are longer-petioled than those of *A. bartramiana.* At flowering time they are often slightly pubescent beneath, and unfold with the flowers, whereas in *A. bartramiana* the glabrous flat leaves precede the flowers. The subglobose fruits have shorter styles, and the top of the ovary shows a tendency to be flattened instead of conical, and the broader and shorter sepals are closely reflexed. Whether *A. neglecta* is really a hybrid, or whether it is a species with a series of somewhat intermediate characters, remains to be proved. Its relative abundance over a fairly extensive area, as well as the apparent constancy of its taxonomic characters, suggests that it is a species of equal rank with *A. laevis, A. fernaldii, A. interior,* and *A. bartramiana.*

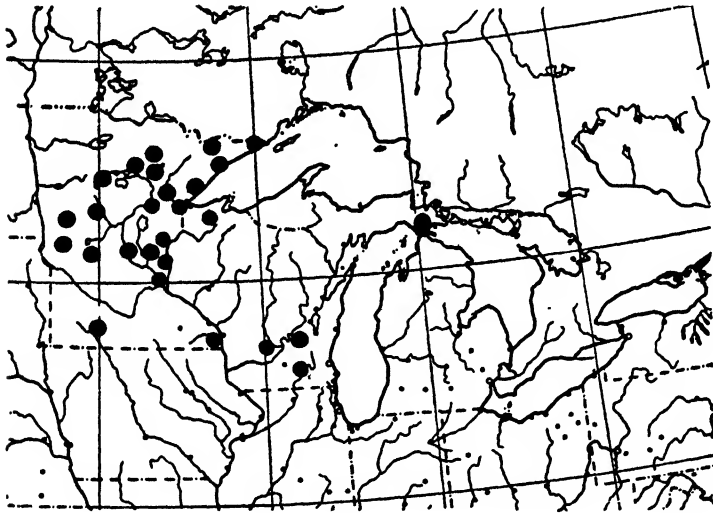## 4. AMELANCHIER INTERIOR Nielsen

(Plates I and VII)

Amelanchier laevis sensu Rosendahl & Butters, Tr. & Shr. Minnesota 217 (1928), ex p. Non Wiegand, 1912.

Amelanchier interior Nielsen in Am. Midl. Nat. 22:185, pl. 13 (1939).

Amelanchier intermedia sensu Nielsen, op. cit. 184, pl. 12, ex p. Non Spach, 1834.

Amelanchier wiegandii Nielsen, op. cit. 180, pl. 10.

Straggling shrubs or small trees up to 8 m. tall; winter buds reddish brown, narrowly ovoid, acute or acuminate, sometimes curved, the lateral 6-9 mm. long, the terminal 8-13 mm. long; bud-scales ciliate; leaves ovate or broadly oval, or elliptical, conduplicate in the bud, unfolded but scarcely fully grown at flowering time, green and sparsely pubescent beneath when young, soon glabrous; mature blades 3-7 cm. long, 2-5 cm. wide, the apex acute or shortly acuminate, the base subcordate or rounded, usually quite glabrous on both surfaces when fully mature; lateral veins 8-11 pairs, not prominent, regularly arranged, usually curved upward and becoming indistinct before reaching the margin; margins finely and evenly serrate or serrulate nearly or quite to the base; teeth 5-6 per cm., 20-30 on each side of average leaves; stipules linear, pubescent, deciduous; petioles slender, 1.5-3 cm. long, glabrous at maturity; flowers in loose, nodding, glabrous, 7-12-flowered racemes 4-7 cm. long, the lower pedicels 12-25 mm. long; petals 5, white, oblanceolate or narrowly obovate, obtuse, 8-13 mm. long, 4-5 mm. wide; stamens about 20, the filaments glabrous; anthers 0.6-0.8 mm. long; hypanthium broadly cup-shaped, 3-5 mm. in diameter, glabrous outside, slightly constricted on the young fruit; sepals triangular-lanceolate, 3-3.5 mm. long, acuminate, pubescent within, usually recurved from the middle after anthesis; styles 5, glabrous, 3-4 mm. long, usually united to the middle; top of the ovary densely white-tomentose; mature fruit globose, purplish black, glaucous, glabrous, 6-8 mm. in diameter, sweet, juicy, edible; lower pedicels 2-4 cm. long; seeds brown, smooth, obliquely lanceloid, somewhat flattened, about 5 mm. long, 2-3 mm. wide.

TYPE LOCALITY: "East River road at junction with Seymour Avenue, S. E. Minneapolis," Hennepin County, Minnesota. Collected in 1935 by Etlar L. Nielsen. Type in the Herbarium of the University of Minnesota.

RANGE: Dry open woods, sandy wooded slopes, or on wooded bluffs along rivers, Minnesota, Wisconsin, and northern Michigan. Flowering in May and June; fruits maturing in July and August.

MINNESOTA: Caribou Lake, *Nielsen* 1379 (Minn.); Tofte, *Breckenridge & Nielsen* 3161 (Minn.); Clarks Bay, Grand Portage, *Breckenridge, Nielsen, & Moore* 3229 (TYPE of *A. wiegandii*, Minn.), *Moore & Nielsen* 3653 (Minn.); Grand Rapids, *Nielsen* 1060, 1063, 1064, 1066, 1069 (Minn.); Cohasset, *Nielsen* 1055 (Minn.); Two Harbors, *Nielsen* 1376 (Minn.); Finland, *Moyle & Nielsen* 1944 (Minn.); Baptism River, *Nielsen* 3170 (Minn.); Itasca Park, *Nielsen* 1931, 2485, 2521, 2547, 3113, 3124, 3127, 3129, 3131, 3133, 3136, 3137, 3138, *Grant* 2862 (GH); Detroit Lakes, *Zech* 152, 161, 168, 195 (Minn.); Carlton, *A. & E. Mattioli* 7, 13, 20 (Minn.); Pelican Rapids, *Butters* 1342 (Minn.); Perham, July 13, 1926, *Rosen-*

MAP 3.—Range of *Amelanchier interior.*

dahl (GH); St. Cloud, *Nielsen* 2669 (Minn.); Center City, July 1892, *Taylor* (GH); Coon Lake, *Nielsen* 1091, 1301 (Minn.); Ham Lake, *Nielsen* 1082 (Minn.); St. Paul, *Rosendahl & Butters* 2578 (GH); Minneapolis, *Nielsen* 2961 (TYPE, Minn.); Mendota, *Rosendahl* 5198 (Minn.); Hastings, *Nielsen* 1820 (Minn.); Red Wing, *Nielsen* 1804 (Minn.); Spring Grove, *Rosendahl* 439, 4935 (GH), 4937 (AA), *Rosendahl & Butters* 3892 (GH).

WISCONSIN: Delton, *Fassett* 2825 (GH); Milford, *Fassett* 7128 (GH); Devils Lake, *Fassett* 3051 (GH); Drummond, *Cheney* 4447 (GH).

MICHIGAN: Foley Creek, near St. Ignace, Mackinac Co., *Benner* 6708 (GH).

This shadbush has the general aspect of *Amelanchier laevis* Wieg., but differs from that species in its smaller stature, wool-top ovary, somewhat shorter fruiting pedicels, and in the smaller flowers in shorter racemes. Until it was described as a distinct species by Nielsen in 1939 it had been variously labeled *A. laevis, A. sanguinea,* or *A. arborea,* or as a hybrid between *A. bartramiana* and *A. sanguinea,* or between *A. laevis* and *A. spicata.*

The leaves at flowering time are usually unfolded but not fully grown, and in the majority of specimens the lower surface is sparsely floccose-pubescent, varying to nearly or quite glabrous. Only rarely do the leaves at this time remain folded and retain sufficient pubescence to give them a whitish or grayish appearance, but by the time the petals have dropped, this tardily-retained pubescence has disappeared.

Amelanchier wiegandii Nielsen is regarded as a synonym of *A. interior.* In the original publication it appears in the key next to *A. interior,* from which it is said to differ in the carinate blades and acute sinuses of the leaf-teeth. These characters are, however, quite intangible. In a tabular comparison it was contrasted with *A. sanguinea,* from which it is widely separated.

5. AMELANCHIER LAEVIS Wieg.

(Plates I and VI)

Pyrus botryapium sensu Bigelow, Fl. Bost. 120 (1814), (ed. 2) 196 (1824). Non L.f. 1781, nec *Amelanchier botryapium* Borkh. 1803.

Amelanchier canadensis sensu Torrey & Gray, Fl. N. Am. 1:473 (1840); Watson & Coulter in Gray, Man. (ed. 6) 166 (1889); Sargent, Silva N. Am. 4:127, pl. 194 (1892); Britton & Brown, Illustr. Fl. N. U.S. 2:237, fig. 1985 (1897); Clark in Bull. Vermont Agr. Exp. Sta. 73:68 (1899); Britton, Man. 517 (1901), (ed. 3) 517 (1907); Small, Fl. Se. U.S. 531 (1903); Sargent, Tr. N. Am. 360 (1905); Robinson & Fernald in Gray, New Man. Bot. (ed. 7) 459 (1908); Britton & Shafer, N. Am. Trees 437 (1908); Jones & Rand in Bull. Vermont Agr. Exp. Sta. 145:99 (1909); Silva Tarouca, Freiland-Laubh. 139, fig. 123 (1913); Coker & Totten, Tr. N. Car. 60 (1916); Farwell in Rep. Mich. Acad. Sci. 17:173 (1916). Non *Mespilus canadensis* L. 1753.

Amelanchier botryapium sensu Emerson, Tr. Massachusetts 443 (1846); Decaisne in Nouv. Arch. Mus. Hist. Nat. Paris 10:135 (1874). Non Borkh. 1803.

Amelanchier canadensis var. *botryapium* Gray, Man. Bot. 130 (1848), (ed. 2) 126 (1856).

Amelanchier lancifolia Hort. ex Hand-list Trees & Shrubs Kew 1:217 (1894), pro syn. *A. canadensis* sensu Torrey & Gray.

Amelanchier stricta Hort. ex ibid.

Amelanchier laevis Wiegand in Rhodora 14:154, pl. 96 (1912); Small & Carter, Fl. Lancaster Co., Pennsylvania 154 (1913); Rehder in Bailey, Stand. Cyclop. Hort. 273 (1914); Deam, Tr. Indiana 177, pl. 76 (1921); Sargent, Man. Tr. N. Am. (ed. 2) 395, fig. 351 (1922); Silva Tarouca, Freiland-Laubh. (ed. 2) 95, fig. 85 (1922); Hoffmann in Proc. Boston Soc. Nat. Hist. 36:280 (1922); Pease in ibid. 37:67 (1924); Bailey, Man. Cult. Pl. 379 (1924); House in N.Y. State Mus. Bull. 254:411 (1924); Wiegand & Eames, Fl. Cayuga Basin 248 (1926); Rehder, Man. Cult. Tr. & Shr. 390 (1927); Sudworth in U.S. Dept. Agric. Misc. Circular 92:134 (1927); Rosendahl & Butters, Tr. & Shr. Minnesota 217 (1928), ex p.; Peattie, Fl. Indiana Dunes 219 (1930); Rydberg, Fl. Prairies & Plains 437 (1932); Deam, Tr. Indiana (ed. 2) 189, pl. 77 (1932); Small, Man. Se. Fl. 636 (1933); Marie-Victorin, Fl. Laurent. 317, fig. 91 (1935); Coker & Totten, Tr. Se. States 208 (1936); Nielsen in Am. Midl. Nat. 22:188, pl. 14 (1939); Deam, Fl. Indiana 532 (1940); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 389 (1940); G. N. Jones, Fl. Illinois 154 (1945); Weatherby & Adams in Contr. Gray Herb. 158:50 (1945).

Amelanchier laevis f. *nitida* Wiegand in Rhodora 13:155 (1912).

Amelanchier laevis var. *cordifolia* Ashe in Journ. Elisha Mitchell Sci. Soc. 34:138 (1918).

Amelanchier laevis var. *nitida* Fernald in Rhodora 23:267 (1922).

A small tree 10-13 m. tall, or a shrub, with spreading branches; bark reddish brown, longitudinally fissured in age; twigs slender, glabrous; winter buds lanceoloid, the scales ciliate; leaves of firm texture, ovate or oval, varying to slightly obovate, conduplicate in the bud, glabrous or nearly so from the first, often bronzy, about half-grown at flowering time, folded lengthwise and glaucous-purplish, soon entirely glabrous, and when mature dark green and slightly glaucous; mature blades 4-6 cm. long, 2.5-4 cm. wide, short-acuminate or acute at the apex, rounded or subcordate at the base; lateral veins 12-17 pairs with short intermediate ones, unequally distant, sinuous, slightly upcurving, anastomosing near the margin, the uppermost widely spreading; margins finely and sharply serrate nearly

to the base, the teeth subulate, callus-tipped, 6-8 per cm., 35-45 on each margin of average leaves; stipules and bracts purplish green, deciduous, sericeous; petioles slender, 12-25 mm. long; flowers large and showy; racemes many-flowered, flexuous, spreading or drooping, 4-12 cm. long, glabrous or nearly so; pedicels glabrous, slender, the lower 1.5-3 cm. long; petals white, oblanceolate or narrowly oval, obtuse, 12-22 mm. long, 3-4 mm. wide; stamens about 20, 3-4 mm. long, the filaments glabrous; anthers 1 mm. long; hypanthium campanulate, 3-5 mm. broad, glabrous, very slightly or not at all constricted below; sepals lanceolate, 3-4 mm. long, acuminate, glabrous outside, tomentulose within, becoming reflexed on the fruit, or sometimes merely divaricate; styles 5, glabrous, 3-4 mm. long, free to below the middle; summit of the ovary glabrous; fruit globose, purple or nearly black, 6-8 mm. in diameter, glaucous, sweet, succulent, edible; lower pedicels 2-5 cm. long; seeds chestnut brown, smooth, asymmetrically ovoid or semi-ellipsoid, somewhat compressed, 4-4.5 mm. long, 2-2.5 mm. wide when fully developed.

TYPE LOCALITY: Wellesley, Massachusetts. Collected by K. M. Wiegand, May and June, 1911. Type in the Gray Herbarium of Harvard University.

RANGE: In dry open woodlands, roadside thickets, cool ravines and hillsides, or damp wooded slopes and banks, from Newfoundland to Minnesota, southward to Missouri, Indiana, and Georgia; flowering in the southern part of the range from the middle of April, in the north to the middle of June; fruit ripe in June and July. Common names: serviceberry, juneberry, maycherry.

QUEBEC: Bolton, July 25, 1926, *Knowlton* (GH); Longueuil, *M.-Victorin* 4319 (AA, GH), 11219, 9503 (AA); Caughnawaga, May 27, 1900, *Jack* (AA); Bic, *Fernald & Pease* 25135 (GH), *Louis-Marie, et al.* 34433 (GH); La Trappe, *Louis-Marie* 145 (GH); Berthier-en-Bas, *Rousseau* 24549 (GH); Saint-Raphael, *Rousseau* 24567, 24562, 24559 (GH); Kingsmere, *Macoun & Malte* 88016 (GH); Shawnigan Falls, *Chamberlain & Knowlton* in 1923 (GH).

NEWFOUNDLAND: Donovans, *Fernald & Wiegand* 5755 (GH); St.-Pierre, *Arsène* 310 (GH); near St. Johns, *Bishop* 373 (GH), *Fernald & Wiegand* 5567, 5568, 5569, 5570, 5580 (GH); Whitbourne, *Fernald & Wiegand* 5545, 5547, 5578a (GH); Cape St. George, *Mackenzie & Griscom* 11102 (GH); French Island, *Fernald, Long, & Fogg* 290 (GH); Lomond, *Fernald, Long, & Fogg* 1791 (GH); Grand Falls, *Fernald & Wiegand* 5552 (GH); Rushy Pond, *Fernald & Wiegand* 5542, 5599 (GH).

NEW BRUNSWICK: Shediac Cape, July 25, 1914, *Hubbard* (GH); Kent, May 30, 1870, *Fowler* (GH).

NOVA SCOTIA: Boylston, *Hamilton* in 1890 (GH); Newport, *Dill* in 1894 (AA); Truro, *Jack* 628 (AA); Middleton, *Long* 21447 (GH), 21448 (GH, AA); Cape Breton Island, *Macoun* 19043 (GH), *Nichols* 557, 168 (GH); Digby, *Howe & Lang* 265, 297 (GH); Marshalltown, *Jack* 3187, 3188 (AA); Meteghan, *Fernald & Long* 21451 (GH); Weymouth, *Fernald, et al.* 21441 (GH), 21442 (GH, AA); Armdale, *Fernald, Bartram, & Long* 23943, 23944, 24761 (GH); Halifax, *Jack* 680, 3648, 3671 (AA).
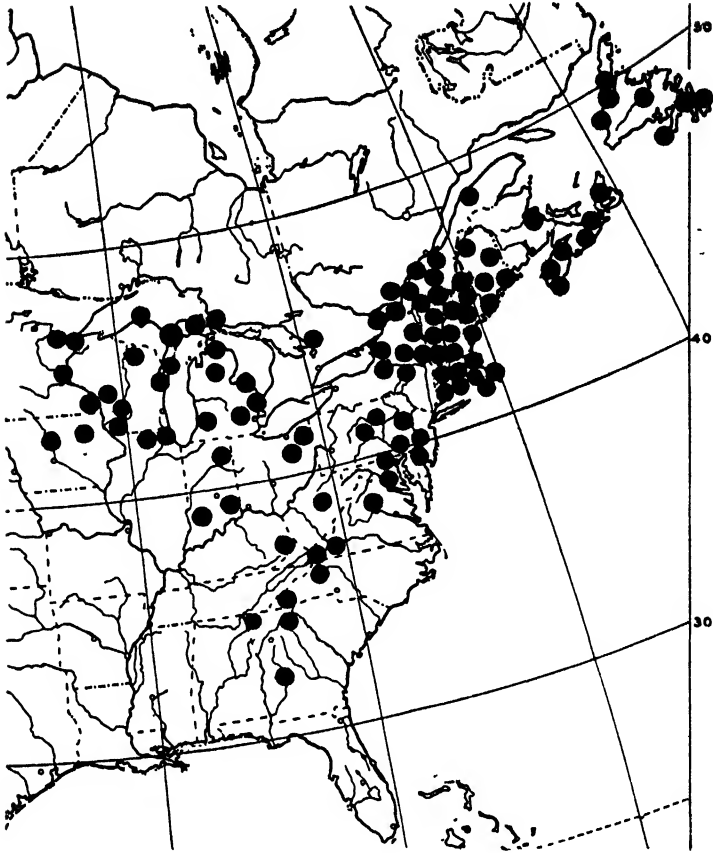
MAP 4.—Range of *Amelanchier laevis.*

PRINCE EDWARD ISLAND: Bothwell, *Fernald & St. John* 11082 (GH).

MAINE: Boothbay, *Fassett* 446 (NE), *Grover & Smith* in 1922 (UI); Kennebunkport, *Koehler* 2 (GH); North Berwick, May 1894, *Parlin* (GH); Vassalboro, *Chamberlain* 34 (NE); South Poland, *Furbish* in 1895 (NE); Mt. Livermore, *Furbish* in 1896 (NE); Monticello, *Fernald & Long* 13763 (AA, NE); Brunswick, *Furbish* in 1892 (NE), May 19, 1897, *Chamberlain* (NE); Cumberland, *Chamberlain* 533 (NE); West Baldwin, *Furbish* in 1900 (NE).

NEW HAMPSHIRE: Mason, May 15, 1915, *Batchelder* (NE); Lebanon, May 3, 1889, *Kennedy* (GH, NE); Peterboro, *Batchelder* 3 (NE); Mt. Agassiz, *Collins* in 1871 (NE); Whitefield, July 4, 1896, *Deane* (NE); Stark, *Pease* 17476 (NE); Franconia, *Faxon* in 1892 (GH, NE); Hooksett, July 11, 1926, *Batchelder* (NE); Dover, *Hodgdon* 195, 2244, 2245 (NE); Barrington, *Hodgdon & Dunn* 2772 (NE); Gorham, *Pease* 16010 (NE); Jaffrey, July 19, 1891, *Deane* (GH, NE).

VERMONT: Pownal, *Floyd* 845 (NE); Sunderland, May 18, 1935, *Pease* (NE); Peacham, May 10, 1889, *Blanchard* (NE); Burlington, May 24, 1914, *Knowlton* (NE); Brunswick Springs, *Sanford* 1066 (NE); Island Pond, *Sanford* 1193 (NE); Johnson, June 3, 1895, *Grout* (NE); Barton, May 24, 1923, *Knowlton* (NE); Willoughby, May 28, 1904, *Kennedy* (NE); Roxbury, *Winslow*, July 18, 1916 (NE); Jamaica, *Moldenke* 9502 (UI); Stratton, June 25, 1914, *Wheeler* (NE); Hartford, June 12, 1920, *Eaton & St. John* (NE).

MASSACHUSETTS: Barnstable, *Child, Knowlton, Bird, & Bean* 16377 (NE); Oak Bluffs, *Seymour* 1224 (GH, NE); Chilmark, *Seymour* 1223 (GH, NE); Mag-

nolia, *Weatherby & Perry,* May 12, 1936, Pl. Exsicc. Gray. 663, 664 (GH, UI); Wellesley, *Wiegand* 2136 (GH, TYPE of *A. laevis*); Coleraine, May 11, 1912, *Batchelder, Kennedy, & Williams* (NE); Whately, *Harger & Fernald,* May 17, 1913 (NE); Granville, *Knowlton & Hunnewell* in 1913 (NE); Amherst, *Seymour* 3501 (NE); Ayer, *Ordway & Bullard,* May 30, 1934 (NE); Nantucket I., *Bicknell* 4835 (NE); Plymouth, *Fernald & Hunnewell* 15192 (NE); Dorchester, May 5, 1889, *Churchill* (NE); Florida, *Fernald & Long* 9623 (NE, GH); Lanesboro, May 22, 1916, *Churchill* (NE); Becket, *G. N. & F. F. Jones* 13716, 13750, 13781, 15323 (UI).

CONNECTICUT: Oxford, *Harger* 3 (GH); Stratford, *Eames* 1 (GH); Southington, *Bissell* in 1901 (GH); Groton, *Graves* in 1901 (GH); Winchester, *Harger* 10 (GH); Waterbury, *Blewitt* 1512 (NE); Glastonbury, *Weatherby* 2861 (NE); Oly Lyme, *Woodward* in 1918 (NE); Andover, *Weatherby* 5280 (NE); Middletown, *Blewitt* 1798 (NE); Hamden, *Blewitt* 1797 (NE).

RHODE ISLAND: Westerly, Aug. 21, 1913, *Bissell, Harger, & Weatherby* (NE); Little Compton, July 27, 1919, *Collins* (NE); Barrington, May 30, 1911, *Winslow* (NE); Cumberland, *Hunnewell* 4129 (NE); Providence, *Collins* in 1902 (GH); Hopkinton, *Fernald, Woodward, & Collins* in 1919 (NE); Smithfield, *Chamberlain* 52 (NE, AA); Prudence Island, *Sanford* 10215 (NE); Lincoln, *Fernald* 9624 (NE).

NEW YORK: Hudson Falls, April 27, 1915, *Burnham* (GH); French Mt., *Burnham* 12 (GH); Judd's Falls, *Wiegand* 2572 (AA, GH); Newcomb, *House* 7961 (GH); North Harpersfield, *Topping* 223 (UI); Stockholm, *Phelps* 1591 (GH); Canton, *Phelps* 567 (GH).

NEW JERSEY: Palmyra, *Long* 14522, 16257 (Ph); Georgia, *Long* 52074 (Ph); Sharptown, *Long* 18378 (Ph); Green Creek, *Stone* 11932 (Ph).

PENNSYLVANIA: Saylorsburg, *Long* 6633 (GH); Lancaster Co., April 25, 1891, *Heller* (GH, Ph); Pocono Plateau, *Harshberger* in 1904 (GH); Reitz Gap, *Wahl* 29 (GH); Trout Run, *Wahl* 298 (GH); Slateford, *Long* 50001 (Ph); Bake Oven Knob, *Pretz* 2363a, 3246 (Ph); Trexlertown, *Pretz* 5919 (Ph); Alburtis, *Pretz* 9090 (Ph); Fleetwood, *Long* 12515 (Ph); Lenhartsville, *Long* 12867 (Ph); Huffs Church, *Wilkens* 6666 (Ph); Schubert, *Wilkens* 5129 (Ph); Nockamixon Narrows, *Benner* 2393 (Ph); Smithville, *Tanger* 3036 (Ph); Brickerville, *Tanger* 3044, 3045 (Ph); Gap, *Long* 30691 (Ph); Hopeland, *Long* 41781 (Ph); Unionville, *Pennell* 82 (Ph); Nottingham Barrens, *Pennell & Long* 7559 (Ph); Landenburg, *Long* 8476 (Ph); St. Peters, *Long* 33631 (Ph); Exton, *Long* 32022 (Ph); Elam, *Long* 32349 (Ph).

DELAWARE: Vandyke, *Long* 48444 (GH, Ph); Coochs Bridge, *Benner* 9567 (Ph); Centreville, June 13, 1898, *Commons* (Ph); Newark, May 11, 1922, *Meredith* (Ph).

MARYLAND: Baltimore, May 15, 1910, *Churchill* (GH); Golt, Montgomery Co., *Hunnewell* 5885 (GH); Elkton, *Randolph* 121 (GH); Elk Neck, *Pennell* 24805 (Ph); North East, *Long* 54418, 57028 (Ph).

WEST VIRGINIA: Canaan Valley, July 21, ——, *Burke* (AA).

DISTRICT OF COLUMBIA: Brightwood, *Smiley* in 1881 (GH).

VIRGINIA: Hopewell Gap, *Allard* 4353 (GH); White Top Mt., *Britton & Vail* in 1892 (AA), June 28, 1892, *Small* (GH); Brushy Mt., June 17, 1892, *Small* (GH).

NORTH CAROLINA: Highlands, *Harbison* 2 (AA); Macon Co., *Harbison* 510, 913 (AA).

GEORGIA: Rabun Co., *Duncan* 3282 (GH); Trenton, *Hermann* 10191 (GH).

ONTARIO: Cornwall, May 28, 1913, May 29, 1914, *Jack* (AA).

MINNESOTA: Mabel, *Spondee* in 1928 (AA); Duluth, July 1, 1914, *Butters* (GH); near Minneapolis, *Nielsen* 1868 (Minn.); Ham Lake, *Nielsen* 1872 (Minn.); Lake City, *Rosendahl & Nielsen* 1852 (Minn.).

WISCONSIN: Black Falls, July 6, 1914, *Lake* (AA); Mud Bay, *Pease* 18044 (GH); Devils Lake, May 25, 1899, *Cheney* (GH); Trout Lake, *Fassett* 13745 (GH); Kilburn, June 1, 1893, *Pammel* (AA); Brown Co., *Schuette* in 1904 (AA); Barneveld, *Fassett* 2826 (GH).

MICHIGAN: Wolverine, *Gleason* 708 (AA); Grayling, *Piper* in 1922 (AA); Port Huron, May 17, 1912, *Dodge* (AA); Mackinac I., July 4, 1912, *Hunnewell* (GH); Sault Ste. Marie, *Newins* 8141 (AA); Ann Arbor, *Hermann* 6471 (GH); Homestead, *Hermann* 7259 (GH); Gwinn, June 6, 1909, *Harrison* (GH); Lansing, *Bailey* in 1887 (GH); Keweenaw Co., *Farwell* in 1889 (GH).

OHIO: Portage Co., *Webb* 1180 (GH); Berea, May 1897, *Watson* (UI).

KENTUCKY: Lynch, *McFarland* 18 (GH).

INDIANA: Miller, *Chase* 197 (UI); Martin Co., *Deam* 12868 (GH); Versailles, *Deam* 16116 (AA); Albion, *Deam* 33798 (AA).

ILLINOIS: Lake Forest, *Harper* in 1890 (AA); Oregon, May 16, 1883, *Waite* (UI); Wabash Co., *Schneck* in 1883 (UI); Lake Zurich, *Hill* 321889 (UI); Barrington, *Chase* 1047 (UI).

IOWA: Fayette, *Fink* in 1894 (GH); Decorah, Aug. 5, 1933, *Tolstead* (Minn.).

Amelanchier laevis is the most noticeably ornamental and graceful of the eastern American serviceberries, and it is rather surprising that such a common and conspicuous species should not have received a specific name until so treated by Wiegand in 1912. It is most closely related to *A. arborea*. Besides its glabrous or nearly glabrous leaves, that are often more or less purplish tinged when young, it differs from *A. arborea* in the more spreading branches, and in the slender, flexuous, pendulous, looser inflorescence and somewhat larger flowers. The mature leaves are usually more abruptly pointed than those of *A. arborea*, rounded (scarcely cordate) at the base, and the blades are green above, paler beneath, and completely glabrous almost from the first. In general, it may be noted. that it has somewhat longer petals, narrower sepals, and the fruits are longer-pedicelled, more succulent, and of a sweeter flavor. The seeds of *A. laevis* are very similar to those of *A. arborea*, but in a large series show a tendency to be very slightly smaller, lighter brown, and somewhat smoother. This trend is, however, not sufficiently tangible for descriptive purposes.

6. AMELANCHIER ARBOREA (Michx.f.) Fern.

(Plates I and VIII)

Mespilus nivea Marshall, Arbustr. Am. 90 (1785), nomen dubium.

Pyrus botryapium sensu Wangenheim, Nordam. Holzarten 90, pl. 28 (1787); Tausch in Flora 21:714 (1838). Non L.f. 1781.

Amelanchier canadensis sensu Walter, Fl. Carol. 148 (1788); Darlington, Fl. Cestrica (ed. 3) 86 (1853); Sargent, Silva N. Am. 4:127, pl. 194 (1892), ex p.; Dippel, Handb. Laubh. 3:392 (1893); Britton & Brown, Illustr. Fl. N. U.S. 2:237, fig. 1985 (1897); Mohr in Contr. U.S. Nat. Herb. 6:545 (1901); Mackenzie & Bush, Man. Fl. Jackson Co., Missouri 108 (1902); Keeler, Our Native Tr. 153 (1902); Small, Fl. Se. U.S. 531 (1903); Card in Bailey, Cyclop. Am. Hort. 57 (1904); Dame & Brooks, Handb. Tr. New Engl. 116, pl. 59 (1904); Sargent, Man. Tr. N. Am. 360, fig. 283 (1905); Blanchard in Torreya 7:97 (1907); Hough, Handb. Tr. N. States & Canada 243, figs. 282, 283, 284 (1907); Emerson & Weed, Our Tr. 191 (1908); Britton & Shafer, N. Am. Tr. 437, fig. 383 (1908); Rogers, Tree Book, pl. opp. p. 298 (1908); Apgar, Ornam. Shr. U.S. 182, fig. 277 (1910); Blakeslee & Jarvis, in Bull. Storrs Agr. Exp. Sta. 69:492-493 (1911); Stone, Pl. So. N.J. in Rep. N.J. State Mus. 1910:488 (1911);

Clements, Rosendahl, & Butters, Minn. Tr. & Shr. 151 (1912); Wiegand in
Rhodora 14:150, pl. 96, fig. 6 (1912); Silva Tarouca, Freiland-Laubh. 139,
fig. 123 (1913); Britton and Brown, Illustr. Fl. N. U.S. (ed. 2) 2:292, fig. 2329
(1913); Small, Florida Tr. 30 (1913); Small, Shr. Florida 29 (1913);
Rehder in Bailey, Stand. Cyclop. Hort. 273 (1914); Bean, Tr. & Shr. Brit. Isles
1:188 (1914); Burns & Otis in Bull. Vermont Agr. Exp. Sta. 194:145 (1916);
Rydberg, Fl. Rocky Mts. 446 (1917); Hitchcock & Standley, Fl. Dist. Columbia
178 (1919); Sargent, Man. Tr. N. Am. (ed. 2) 394, fig. 350 (1922); Hoffmann
in Proc. Boston Soc. Nat. Hist. 36:280 (1922); House, N.Y. State Mus. Bull.
254:411 (1924); Bailey, Man. Cult. Pl. 379 (1924); Wiegand & Eames, Fl.
Cayuga Basin 248 (1926); Rehder, Man. Cult. Tr. & Shr. 390 (1927); Sud-
worth in U.S. Dept. Agric. Misc. Circular 92:134 (1927); Pepoon, Fl. Chicago
Area 342 (1927); Rosendahl & Butters, Tr. & Shr. Minnesota 218 (1928);
Miller & Tehon, Native & Naturalized Tr. Illinois 203, pl. 66 (1929); Peattie,
Fl. Indiana Dunes 219 (1930); Rydberg, Fl. Prairies & Plains 436 (1932);
Deam, Tr. Indiana (ed. 2) 189, pl. 76 (1932); Small, Man. Se. Fl. 636 (1933);
Palmer & Steyermark in Ann. Missouri Bot. Gard. 22:557 (1935); Marie-
Victorin, Fl. Laurent. 316, fig. 91 (1935); Griscom in Rhodora 38:48 (1936);
Coker & Totten, Tr. Se. States (ed. 2) 207 (1937); Munns in U.S. Dept. Agric.
Misc. Publ. 287:137, pl. 133 (1938); Nielsen in Am. Midl. Nat. 22:183, pl. 11
(1939); Steyermark, Spring Fl. Missouri 255, pl. 68, fig. 1 (1940); Rehder,
Man. Cult. Tr. & Shr. (ed. 2) 388 (1940); Deam, Fl. Indiana 532 (1940). Non
Mespilus canadensis L. 1753.

Mespilus amelanchier β nivea Castiglioni, Viagg. St. Uniti 2:293 (1790).

Mespilus canadensis var. *β cordata* Michx. Fl. Bor. Am. 1:291 (1803).

Mespilus arborea Michx.f. Hist. Arb. Am. Sept. 3:68, pl. 11 (1810), N. Am. Sylva
2:70, pl. 66 (1818), (ed. 3) 2:60, pl. 66 (1859).

Aronia arborea Barton, Comp. Fl. Philadelphia 1:228 (1818).

Aronia botryapium sensu Elliott, Sketch Bot. S. Car. & Ga. 1:557 (1821). Non Pers.
1807.

Amelanchier ovalis var. *β subcordata* DC. Prodr. 2:632 (1825).

Aronia subcordata Rafinesque ex DC., ibid.

Malus microcarpa Rafinesque ex DC., ibid.

Aronia cordata Rafinesque, Med. Fl. 2:196 (1830) nom. nud.

Amelanchier botryapium sensu Spach, Hist. Nat. Veg. Phan. 2:85 (1834); Torrey,
Fl. N. Mid. States 203 (1826); Darlington, Fl. Cestrica 294 (1837); Farwell in
Rep. Mich. Acad. Sci. 17:175 (1916). Non Borkh. 1803.

Pyrus wangenheimiana Tausch in Flora 21:715 (1838).

Aronia nivea Neumann ex Tausch, ibid.

Amelanchier canadensis var. *a botryapium* Torrey & Gray, Fl. N. Am. 1:473 (1840);
Torrey, Fl. N.Y. 1:225 (1843); Walpers, Rep. Bot. Syst. 2:55 (1843); Gray,
Man. Bot. 130 (1848); Brendel, Fl. Peoriana 47 (1887); Chapman, Fl. S. U.S.
(ed. 3) 141 (1897); Schneider, Illustr. Handb. Laubh. 1:734, fig. 409 (1906);
Robinson & Fernald in Gray, New Man. Bot. (ed. 7) 460 (1908).

Amelanchier wangenheimiana M. Roem. Syn. Mon. 3:146 (1847).

Amelanchier canadensis var. *tomentula* Sargent, Man. Tr. N. Am. 361 (1905);
Schneider, Illustr. Handb. Laubh. 1:734 (1906); Robinson & Fernald in
Rhodora 11:47 (1909).

Amelanchier intermedia sensu Blanchard in Torreya 7:98 (1907), ex p. Non
Spach 1834.

Amelanchus canadensis Vollmann, Fl. Bayern 453 (1914).

Amelanchier canadensis f. *nuda* Palmer & Steyermark in Ann. Missouri Bot. Gard.
25:772 (1938); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 388 (1940).

Amelanchier arborea Fernald in Rhodora 43:563, pl. 672, fig. 2 (1941); G. N.
Jones, Fl. Illinois 154 (1945).

*Amelanchier austromontana* sensu Fernald in op. cit. 566. Non Ashe 1918.

A small tree 5-20 m. tall, with a maximum trunk diameter of 40 cm., or an irregularly branched shrub, the stems solitary or few together, not growing in clumps; branches ascending; bark grayish brown, longitudinally fissured on old stems, that of the young stems gray, smooth, and often somewhat striped; twigs of the season pubescent at first, soon glabrous, brown and slightly glossy; winter-buds lanceoloid, acuminate, glabrous; leaves conduplicate in the bud, small, densely white-tomentose, mostly folded at flowering time; blades 4-10 cm. long, 2-2.5 cm. wide, ovate or oval, or slightly obovate, short-acuminate or acute at the apex, cordate or rounded at the base; mature leaves thick, firm, dark green and glabrous above, paler beneath and pilose at least along the midvein, becoming nearly or quite glabrous in age; lateral veins 11-17 pairs, unequally distant, sinuous, anastomosing and indistinct toward the margin; margins sharply and finely and often somewhat doubly serrate almost or quite to the base, the teeth ascending, incurved, slender, 6-10 per cm., mostly 50-60 on each side of average leaves; stipules linear, caducous, pilose; petioles 1-2 cm. long; flowers 2-2.5 cm. in diameter, fragrant, appearing early, usually before the leaves have unfolded; racemes spreading or somewhat pendulous, 4-10 cm. long, 4-10-flowered; pedicels grayish pubescent, the lower 8-17 mm. long; petals oblanceolate, 12-18 mm. long, 2-5 mm. wide, white, or sometimes pinkish; stamens about 20, 3-4 mm. long, the filaments glabrous; anthers 0.6-0.8 mm. long; hypanthium campanulate, 2.5-3 mm. in diameter, glabrous or somewhat floccose; sepals triangular-lanceolate, acute, 2-3 mm. long, tomentulose on both sides, becoming strongly reflexed from the base after anthesis; styles 5 (or 4), about 4 mm. long, glabrous, the free portion 2-3 mm. long; summit of ovary glabrous; fruit globose, purple (rarely whitish), 6-10 mm. in diameter, scanty, somewhat tasteless, falling early; lower pedicels 1-2.5 cm. long; seeds 3-10, dark brown, nearly smooth, glabrous, 4.5-5 mm. long, 2-3 mm. wide when fully developed, asymmetrically lanceoloid, somewhat flattened.

TYPE LOCALITY: "Hab. . . . a Canada ad Virginiam et in montibus Carolinae." Phototypes in the Gray Herbarium and the Arnold Arboretum.

RANGE: In dry woods and open ground, and on wooded hillsides, from Maine to Minnesota, southward to Louisiana and Florida. Flowering from the end of March to the end of May; fruits ripening in June and July.

QUEBEC: Longueuil, *M.-Victorin* 11222 (AA); Aylmer, *Rolland* 57, 58, 59 (GH); Kingsmere, *Macoun & Malte* in 1913 (GH); Ile Bigras, *M.-Victorin* 24547 (GH); Oka, *M.-Victorin* 24546 (GH); Grosse-Isle, *M.-Victorin* 15586 (AA); Montmorency Falls, Aug. 20, 1895, *Jack* (AA).

MAINE: Monhegan Island, *Jenney, Churchill, & Hill* 3264 (NE); Mt. Desert I., *Rand,* July 1899 (NE); Lincolnville, *Rossbach* 1102 (NE); Northport, *Rossbach* 1136 (NE); Orono, *Harvey* in 1898 (UI); Milford, *Fernald* 13767 (GH); West Pembroke, *Fernald* 1885 (GH).
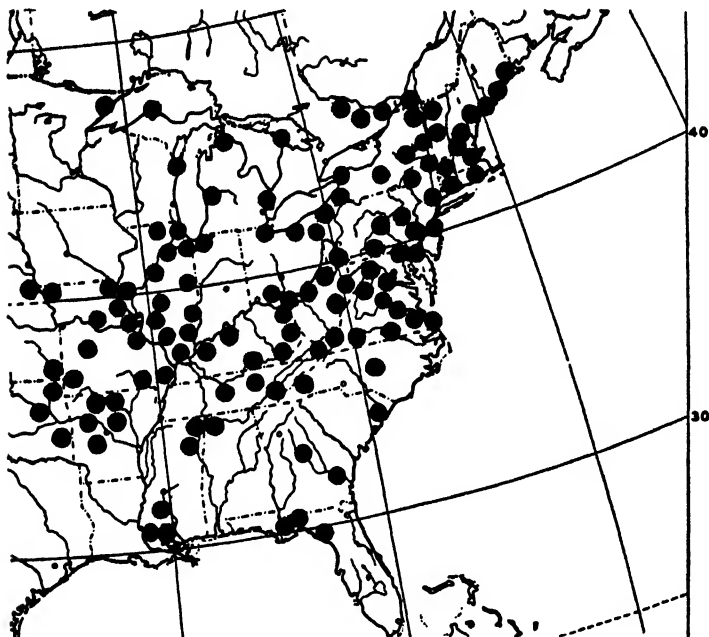
MAP 5.—Range of *Amelanchier arborea.*

NEW YORK: Pavilion, *Hill* in 1859 (UI) ; New York, *Burnham* 1162 (GH) ; New London, *House* 11870 (GH) ; Sylvan Beach, *House,* May 16, 1918 (GH) ; Albany, *House* 7787 (GH) ; Middlefield, *Hunnewell* 6889 (GH) ; Spencer, *Eames & Dean* 4293 (GH) ; Canton, *Phelps* 1581, 1582 (GH) ; Black Rock Forest, *Raup* 7410, 7727 (GH).

VERMONT: Plainfield, *Eggleston* 1959 (GH) ; Twin Mts., *Eggleston* 1182, 1957 (GH) ; Pittsford, *Eggleston* 1183 (GH) ; Townshend, *L. A. Wheeler* in 1915 (GH) ; Charlotte, May 22, 1922, *Knowlton* (NE) ; Newport, May 24, 1923, *Knowlton* (NE) ; W. Fairlee, June 10, 1933, *Anderson, et al.* (NE).

NEW HAMPSHIRE: Walpole, May 26, 1917, *Bean & Fernald* (NE) ; Lebanon, *Fernald, Hunnewell, & Blanchard* in 1920 (NE) ; Wolfboro, *H. E. Sargent* 24 (GH).

MASSACHUSETTS: Canton, May 5, 1895 *Williams* (NE) ; Plainfield, June 14, 1913, *Forbes* (NE) ; Brimfield, May 20, 1916, *Knowlton* (NE) ; Montague, May 13, 1911, *Fernald* (GH, NE) ; Erving, *Hunnewell, Macbride, & Torrey,* May 14, 1915 (NE) ; Whately, May 17, 1913, *Harger & Fernald* (NE) ; Shelburne Falls, May 11, 1912, *Bean & Knowlton* (NE) ; West Orange, May 10, 1912, *Hunnewell & Wiegand* (NE) ; Shutesbury, *Tower & Seymour* 3674 (NE) ; Northfield, May 11, 1912, *Fernald & Floyd* (NE) ; Rowe, *Fernald & Long* 9621 (GH) ; Andover, *Pease* 678 (NE).

CONNECTICUT: Waterbury, *Blewitt* 2038 (NE) ; Glastonbury, *Wright* in 1916 (GH) ; Middlebury, Apr. 23, 1896, *Shepardson* (NE) ; Danbury, *Blewitt* 2039 (NE) ; Tariffville, May 17, 1913, *Winslow & Hill* (NE)·; Southington, *Blewitt* 1802 (NE), *Bissell* in 1901 (GH) ; East Hartford, May 18, 1913, *Briggs* (NE) ; Kent, *Eames* 8287 (NE) ; Barkhamsted, *Blewitt* 1805, 3650 (NE) ; Watertown, *Blewitt* 2036, 3501 (NE) ; Winstead, *Blewitt* 1804 (NE) ; Thomaston, *Weatherby* D2157 (NE).

RHODE ISLAND: Portsmouth, June 10, 1911, *Collins* (NE) ; Cumberland, *Hunnewell* 4128 (NE) ; Lincoln, May 30, 1919, *Collins* (NE).

NEW JERSEY: Woodglen, *Long* 52340 (Ph); Penville, *Long* 52160 (Ph); Charlestown, *Long* 46255 (Ph); Little York, *Long* 46808 (Ph); Tumble Falls, *Hermann* 4016 (Ph); Drea Hook, *Long* 53736 (Ph); Bordentown, *Long* 3107 (Ph); Smithville, *Long* 9610 (Ph); Cranbury, *Long* 51868 (Ph); Deerfield, *Long* 32089 (Ph); Pennington, *Long* 50133 (Ph); Palmyra, *Long* 11943, 13516, 14514, 14519 (Ph); Somerdale, *Long* 11605 (Ph).

PENNSYLVANIA: Safe Harbor, Apr. 18, 1889, *Heller* (GH); Lenhartsville, *Wilkens* 1097 (GH); Ohio Pyle, May 21, 1910, *Bartram* (GH); Pleasant Valley, June 9, 1923, *Benner* (GH); Wagontown, Apr. 25, 1925, *Stone* (GH); Reseca Falls, June 9, 1918, *Bartram* (GH); Perkiomen Creek, *Long & St. John* 2479 (GH); Fairview, *Wahl* 34 (GH); Mercersburg, *Adams & Wherry* 4662 (GH); Linfield, *Long* 11883 (GH); Rosscommon Creek, *Long* 6586 (GH); Bernville, *Stoudt & Hermann* 2779, 2784 (GH).

DELAWARE: Deakyneville, *Long* 58228 (Ph); Mount Cuba, *Long* 32282 (Ph).

WEST VIRGINIA: Panther Mt., *Rydberg* 9052 (AA); White Sulphur Springs, *Hunnewell* in 1914 (GH), *Harbison* 7095 (AA); Aaron's Run, Monongalia Co., *Myers* 415 (UI); Ravenswood, May 14, 1939, *Balsar* (GH).

VIRGINIA: Williamsburg, *Grimes* 2560 (GH); Massanutten Mts., *Allard* 4498 (GH); Rye Valley, June 11, 1892, *Small* (GH); Holston River, Aug. 8, 1892, *Small* (AA); Hot Springs, *Hunnewell* 4029 (GH); Wytheville, *Svenson* 7779 (GH); near Wylliesburg, *Palmer* 39994 (AA); near Antioch, *Allard* 2819 (GH); near Aldie, *Allard* 2516, 2584 (GH); Beverly, *Allard* 220 (GH); High Point, *Allard* 4342 (GH); Little Neck, *Fernald & Long* 3959 (GH); Great Neck, *Fernald, Griscom, & Long* 4650 (GH); Pungo, *Fernald & Griscom* 4425 (GH); Indian Point, *Fernald & Long* 11698, 11845 (GH); Clarendon, *Blake* 10557 (GH); Emporia, *Fernald & Long* 8291 (GH, Ph); Cleopus, *Fernald & Long* 13040 (GH, Ph); Surry Courthouse, *Fernald & Long* 13039 (GH, Ph); Richmond, *Fernald & Long* 7063 (GH, Ph); Gary Church, *Fernald & Long* 7064 (GH, Ph); Homeville, *Fernald & Long* 7065 (GH, Ph); Waverly, *Fernald & Long* 7067 (GH, Ph); South Hill, *Fernald & Long* 7069 (GH, Ph); Burt, *Fernald & Long* 7450 (GH, Ph); Ingersoll, *Fernald & Long* 11844 (GH, Ph); Scotland, *Fernald & Long* 13041 (GH, Ph).

MARYLAND: May 16, 1905, *Hitchcock* (UI); Oakwood, *Tanger* 3025 (Ph); Golt, *Tidestrom* 11882 (GH); Bald Friar, *St. John & Long* 1009 (GH), 8059 (Ph); Middle Neck, *Long* 37298 (GH, Ph); Elk Neck, *Long* 37719 (Ph); Providence Mill, *Benner* 4883 (Ph).

NORTH CAROLINA: Linville, *Randolph* 1200 (GH); Salisbury, *Harbison* 6 (AA); Raleigh, *Harbison* 30 (AA); Chapel Hill, *Harbison* 15 (AA); Ridge Crest, *Davis* 1462 (UI).

SOUTH CAROLINA: Santee Canal, *Ravenel,* s.n. (GH); Anderson, *Palmer* 42440 (AA).

GEORGIA: Holton, *Harper* 1806 (GH, AA); N. Georgia, *Wright* in 1875 (GH); Wayne Co., *Eyles* 6894 (GH); Lookout Mt., July 1898, *Ruth* (UI).

FLORIDA: River Junction, *Harbison* 1415 (AA); Round Lake, *Harbison* 4 (AA); Caryville, Mar. 30, 1927, *Hume* (AA); Lake Tamonia, *Griscom* 21578 (GH); Aspalaga Bluff, Apr. 26, 1924, *Small* (GH).

ONTARIO: Niagara, *John Macoun* 34296 (GH); Killaloe, May 1903, *Jack* (A); Stokes Bay, *Krotkov* in 1934 (GH); Belleville, May 16, 1878, *Macoun* (GH).

WISCONSIN: Jacksonport, May 30, 1926, *Kraus, et al.* (GH).

MINNESOTA: Grand Portage, *Nielsen* 1630 (Minn.).

MICHIGAN: Bridgeton, *Hermann* 9625 (AA).

OHIO: Ironton, *Werner* 55 (GH); Toledo, *Sanford* 379 (GH); Garrettsville, *Webb* 84 (GH); Sugar Grove, *Horsey* 323 (AA); Urbana, Apr. 22, 1838, *Samples* (UI); Berea Co., *Watson* in 1897 (UI); Otway, *Demaree* 11260 (AA).

INDIANA: Near Attica, *Deam* 22524 (AA); Liverpool, *Chase* 2035 (UI); Dune Park, *Chase* 2053 (UI); Fountain, *Deam* 23005 (UI); Clarke, *Moffatt* 190 (UI);

Bloomington, *Friesner* 9541 (UI); Pine, May 13, 1876, *Hill* (UI); Portland Arch, *G. N. Jones* 13143 (UI).

ILLINOIS: Camp Grant, *Mattoon* 13 (UI); Marshall Co., *Chase* 1795 (UI); Will Co., *Hill* 411912 (UI); Starved Rock, *Greenman, Lansing, & Dixon* 81 (GH), *Thone* 172 (UI); Peoria, *McDonald* in 1904 (GH, UI); Adams Co., *Evers* 52 (UI); Urbana, Aug. 11, 1899, *Clinton* (GH); Mahomet, Sept. 23, 1899, *Gleason* (GH); Homer, Sept. 16, 1899, *Clinton* (UI); Taylorville, Apr. 22, 1899, *Andrews* (UI); Carlinville, Apr. 12, 1890, *Andrews* (UI); Richland Co., *Ridgway* 2534 (AA); Grand Tower, May 3, 1902, *Gleason* 2404 (GH, UI), 1695 (GH); Wabash Co., Sept. 1886, *Schneck* (UI); Johnson Co., May 26, 1902, *Schneck* (UI); Vermilion River, *G. N. Jones* 13340 (UI); Wolf Lake, *G. N. Jones,* 12089 (UI); Franklin Creek, *G. N. Jones* 15840 (UI); Sangamon River, *G. N. Jones* 15618 (UI); Dixon Springs, *G. N. Jones* 11992 (UI).

MISSOURI: Painton, *Palmer* 34917 (AA); Monticello, *Palmer* 35890 (AA); La Grange, *Davis* 2227 (AA); Kahoka, *Palmer* 25860 (AA); Livonia, *Palmer* 41069 (AA); Thayer, *Palmer* 14684 (AA); Whiteside, *Davis* 49 (UI); Allenton, May 20, 1882, *Letterman* (AA); St. Charles Co., *Drouet* 1421 (AA); Jefferson Co., *Letterman* 2, 3 (AA); Webb City, *Palmer* 1602 (AA); Newton Co., *Palmer* 29927 (AA), *Bush* 85, 3509 (GH); McDonald Co., *Bush* 30, 85a, 85b, 85c (GH); Wright City, *Davis* 1259 (AA); Oronogo, *Bush* 1602 (GH, UI), 1602A (GH); Hannibal, *Davis* 113 (AA), 704 (GH, AA), 2011 (AA, UI), 4646 (UI).

KENTUCKY: Louisville, *Fischbach* 228 (GH); Chalybeate Springs, *Schacklette* 261 (GH); Monticello, *Smith & Hodgdon* 3872 (GH); South Portsmouth, *Demaree* 11245 (AA).

ARKANSAS: Hardinville, *Palmer* 26350 (GH); Hamburg, *Demaree* 18743 (UI); Baxter, *Bush* 15250 (AA); Hot Springs, *Palmer* 24470 (AA); Little Rock, *G. M. Merrill* 1965 (UI); Nogo, *G. M. Merrill* in 1933 (UI); Van Buren, Apr. 29, 1910, *Brown* (AA); Shirley, *Palmer* 33207 (AA); Izard Co., *Palmer* 35564 (AA); Eureka Springs, *Palmer* 5616 (AA).

TENNESSEE: Knoxville, *Ruth* 317 (GH); Spence Field, *Sharp & Svenson* 7278 (GH); Craggie Hope, *Svenson* 346 (GH).

ALABAMA: Huntsville, *Hubricht* B2011 (MBG); Selma, "cultivated and more or less naturalized," *Cocks,* no number or date (AA).

MISSISSIPPI: Rockport, *Harbison* 11 (AA); Tishomingo City, *Harbison* 40 (AA); Mooreville, *Palmer* 39015 (AA).

LOUISIANA: Covington, Apr. 22, 1910, *Cocks* (AA).

NEBRASKA: Nemaha, *Bates* 5992 (AA).

KANSAS: Baxter Springs, *Bush* 10380 (AA, UI).

OKLAHOMA: Near Page, *Palmer* 20761, 20764 (AA); near Ottawa, *Stevens* 2427 (AA); Ottawa Co., *Palmer* 29915 (AA).

Amelanchier arborea is an arborescent species with acuminate, cordate, finely serrate leaves that are pubescent at flowering time, long narrow petals, glabrous ovary, five styles, and somewhat dryish fruits, that has been called *A. canadensis* by many botanists. It is closely related to *A. laevis* and to *A. interior.* The bark is shallowly fissured and grayish brown. When the leaves are about one-third grown the spreading or drooping racemes of white flowers cover the tree. The flowers are therefore conspicuous in early spring when most other trees are leafless. The wood is sometimes used for fishing poles, or for handles for tools. The fruits of *A. arborea,* unlike those of other eastern American species are scanty, scarcely edible, and fall early.

It has been pointed out by M. L. Fernald (Rhodora 43:562-563. 1941) that the first clear account of this species was that of *Mespilus canadensis* var. β *cordata* Michx. 1803. "In 1810, the younger Michaux, evidently taking the name from his father's first word of diagnosis, elevated *M. canadensis* var. β *cordata* to specific rank as *M. arborea* Michx.f. . . . Here, then, is the first perfectly clear name for *Amelanchier canadensis* sensu Wiegand." It is interesting to note, however, that the error of misapplying the name *A. canadensis* to *A. arborea* (Michx.f.) Fern. did not originate with Wiegand in 1912, for no fewer than twenty previous authors had misused the name *A. canadensis* in this sense. Apparently the earliest binomial which might apply to this species is *Mespilus nivea* Marsh. However, Marshall's account, more of a horticultural commentary than a botanical description, "is altogether too vague, unless an original specimen of it can eventually be discovered. Its transfer into Amelanchier would merely lead to the doubt which surrounds so many names unfortunately taken up from Marshall's inadequate and often merely impressionistic accounts." (Fernald, l.c.)

Pyrus wangenheimiana Tausch, based on material growing in the Leibnitz garden at Prag, is represented by a sheet in the Bernhardi Herbarium at the Missouri Botanical Garden, which through the kindness of the curator, Dr. J. M. Greenman, I have had the opportunity of examining. This sheet is probably part of the original Tausch exsiccati and may therefore be regarded as authentic. It has two specimens, one of mature leaves, and the other consisting of a young flowering branch. Although labeled by Wiegand in 1912 "a probable hybrid" between *A. canadensis* (sensu auth.) and *A. laevis* Wieg., it is evidently quite typical *A. arborea* (Michx.f.) Fern.

The leaves of *A. arborea* usually retain even at maturity some pubescence on the lower surface, at least toward the base of the blades and on the petioles. On certain specimens, however, especially those collected from plants in exposed situations, the leaves are not infrequently glabrous at maturity. Such specimens, which in the absence of fruits are sometimes not easily distinguished from *A. laevis*, have been named *A. arborea* f. *nuda* by Palmer & Steyermark.

The taxonomic identity of certain specimens from Westminster, Vermont, collected by W. H. Blanchard in 1903 and 1907, and distributed as "*A. intermedia* Spach" and "*A. saxatilis* Blanchard" is not yet determined. In 1912, Wiegand was confronted with the same problem, which he likewise was apparently unable satisfactorily to solve. The specimens are, as Wiegand has said, difficult to understand because they do not belong to any species now recognized. He suggested that they may have been of hybrid origin, and concluded that they need more study in the

field. With this view I am in complete accord, but am at present unable to add any further clarifying statement beyond the suggestion that possibly the specimens represent hybrids between *A. arborea* and *A. bartramiana.*

6a. AMELANCHIER ARBOREA var. **alabamensis** (Britt.) n. comb.

Amelanchier alabamensis Britton in Britton & Shafer, N. Am. Tr. 439, fig. 386 (1908); Wiegand in Rhodora 14:132, 240 (1912); Small, Man. Se. Fl. 636 (1933).

A small tree resembling *A. arborea,* but differing in the tomentose top of the ovary; flowering specimens unknown.

TYPE LOCALITY: In sandy land three miles south of Auburn, Lee Co., Alabama, Mar. 19, and May 28, 1898, *F. S. Earle & C. F. Baker* 1610 (TYPE, in the herbarium of the New York Botanical Garden).

RANGE: Arkansas and Alabama.

ARKANSAS: Magazine Mt., Logan Co., *Palmer* 23222 (AA).

ALABAMA: Auburn, Lee Co., *Earle & Baker* 1610 (NY); Birmingham, Jefferson Co., *Palmer* 35329, 38948 (AA); Little Mountain, about four miles south of Tuscumbia, Colbert Co., *Harper* 3322 (GH, AA).

Little has been added to the meager knowledge of this peculiar plant since Wiegand studied it in 1912. It is here reduced to the varietal category because it appears probable that it is not a species of equivalent rank with *A. arborea.* Concerning the status of *A. alabamensis,* Wiegand (Rhodora 14:132. 1912) commented as follows: "In 1908 Britton described *Amelanchier alabamensis* from material collected by F. S. Earle and C. F. Baker three miles south of Auburn, Alabama. The writer has seen this material which was distributed by Earle and Baker, both the type specimen and also that which was sent to several other herbaria, but is still unable to form any satisfactory opinion regarding it. At flowering time the young leaves, hypanthium and sepals are like *A. canadensis* [*A. arborea*], but the summit of the ovary is hairy. The mature leaves are not distinctive but are more like those of *A. canadensis* [*A. arborea*]. Nowhere in any of the herbaria studied by the writer are there other specimens which will match these. Thus one is strongly forced toward the opinion that *A. alabamensis* is not a good species of the same grade as those with wide distribution, and that it is to be explained as a local hybrid or as a local environmental variety. Before this conclusion is finally reached however, a more extended search in the Southern States should be made, for this region is one from which little material of Amelanchier finds its way into the herbaria." Later in the same year Wiegand (l.c. 240) concluded that "a certain amount of woolliness on the summit of the ovary must be admitted among the allowable variations of *A. canadensis* [*A. arborea*] without, however, constituting a distinct

variety." In the view of the present writer the most appropriate procedure at present is to treat the Alabama plants as a variety of *A. arborea* until results of field studies are available to shed further light on the understanding of these plants. At the present time flowering specimens are unknown. Until these are at hand it seems inadvisable to relegate *A. alabamensis* to synonymy under *A. arborea,* or to follow Britton & Shafer, and Small in treating it as a distinct species.

6b. × AMELANCHIER GRANDIFLORA Rehd.

Amelanchier canadensis × *laevis* sensu Wiegand.
Amelanchier (?) *botryapium lancifolia* Simon-Louis apud Zabel, Syst. Verz. Muenden 19 (1878), nom. nud.
Amelanchier canadensis grandiflora Zabel in Beissner, Schelle, & Zabel, Handb. Laubh.-Ben. 191 (1903), nom. nud.
Amelanchier lancifolia hort. gall. ex Zabel, ibid., pro syn.
Amelanchier grandiflora Rehder in Journ. Arnold Arb. 2:45 (Sept. 6, 1920) ; Man. Cult. Tr. & Shr. 390 (1927), (ed. 2) 388 (1940).

According to Sax (Journ. Arnold Arb. 12:9. 1931) this is a tetraploid hybrid between *A. arborea* and *A. laevis.* In the original publication, Rehder says that it differs from *A. arborea* in the larger flowers, the longer and more slender, less pubescent racemes, and in the purplish young leaves covered with a dense and more floccose tomentum which soon disappears entirely; from *A. laevis* it differs in the tomentose young leaves, the slightly villous racemes with more numerous flowers on shorter pedicels, and in the larger, more succulent fruit. "Among the many Amelanchiers grown at the Arboretum it is easily the most handsome and always attracts attention by the abundance of its large flowers set off effectively by the purplish foliage; it forms a large tree-like shrub with wide-spreading slender branches. As I saw it in 1893 in the Botanic Garden of the Forest Academy at Muenden it formed a well-shaped small or medium-sized tree with spreading branches; it had been received from the nursery of Simon-Louis near Metz as *A. lancifolia,* a name which apparently was never published." (Rehder, l.c.). Accompanying the original description are a number of citations of specimens which have been referred to this hybrid by Wiegand. While there is little doubt that the plants in cultivation are actually of hybrid origin, almost all the specimens of feral plants that I have examined are clearly referable to either *A. laevis* or *A. arborea.* The following specimens of cultivated plants are in the herbarium of the Arnold Arboretum.

SPECIMENS OF CULTIVATED PLANTS: Bot. Gard. Muenden, April 23 and July 3, 1893, *A. Rehder* (TYPE, AA); Arnold Arb. under no. 4406 (received from Muenden in 1892) May 11, 1900, May 3, 1902, June 22, 1903, May 11 and July 6, 1912, May 14 and July 5, 1919; Arb. Spaeth, Berlin, May 8, 1909, *H. Jensen.*

6c. × AMELANCHIER GRANDIFLORA f. RUBESCENS Rehd.

A. grandiflora f. *rubescens* Rehder in Journ. Arnold Arb. 2:46 (1920), Man. Cult. Tr. & Shr. 390 (1927), (ed. 2) 388 (1940).

Flowers purple-pink in bud, tinged with pink when open.

Cultivated in the Durand-Eastman Park, Rochester, New York; specimens collected: May 16, 1920, *B. H. Slavin & J. Dunbar.*

"This handsome form agrees in its characters with the type except that the flowers are purple-pink in bud and suffused with pink when open. It is a seedling from a tree of typical *A. canadensis* [i.e., *A. arborea*] growing in Seneca Park, Rochester, and represented in our herbarium by specimens collected by B. H. Slavin and marked No. 10. The seedling described above, however, shows unmistakably the influence of *A. laevis* which is growing at the same locality."

7. AMELANCHIER CANADENSIS (L.) Medic.

(Plates II, IX, and X)

Mespilus canadensis L. Sp. Pl. 478 (1753), Syst. Veg. (ed. 13) 388 (1774); Miller, Gard. Dict. (ed. 8) no. 6 (1768).

Mespilus virginiana Miller, Gard. Dict. ed. 8; No. 11 (1768).

Pyrus botryapium L.f. Suppl. Pl. Syst. 255 (1781); Willdenow, Sp. Pl. 2:1013 (1799), Enum. Pl. 525 (1809); Pursh, Fl. Am. Sept. 339 (1814); Sprengel, Syst. Veg. 2:509 (1825).

Crataegus racemosa Lamarck, Encycl. Méth. Bot. 1:84 (1783); J. St. Hil. Expos. Fam. Nat. 2:182 (1805); Poiret in Lamarck, Encycl. Méth. Bot. Suppl. 1:292 (1810).

Amelanchier canadensis (L.) Medicus, Gesch. 79 (1793); Michaux, Fl. Bor. Am. 1:291 (1803); K. Koch, Dendrol. 1:180 (1869); Fernald in Rhodora 43:566, pl. 672, fig. 1 (1941); Weatherby & Adams in Contr. Gray Herb. 158:50 (1945).

Crataegus amoena Salisbury, Prodr. Stirp. Chap. Allert. 357 (1797), nomen illegit.

Amelanchier botryapium Borkhausen, Theor.-prakt. Handb. Forstb. 2:1260 (1803); DC. Prodr. 2:632 (1825); Hooker, Fl. Bor. Am. 1:202 (1834); Britton & Brown, Illustr. Fl. N. U.S. 2:238, fig. 1986 (1897); Mohr in Contr. U.S. Nat. Herb. 4:545 (1901); Card in Bailey, Cyclop. Am. Hort. 57 (1904); Britton, Man. Fl. N. States 517 (1901), (ed. 3) 517 (1907); Small, Fl. Se. U.S. 531 (1903); Keeler, Our Northern Shr. 192 (1903); Coker & Totten, Tr. N. Carol. 59 (1916).

Aronia botryapium Persoon, Syn. Pl. 2:39 (1807); Nuttall, Gen. Am. Pl. 306 (1818); Torrey, Fl. N. & Mid. U.S. 1:479 (1824); Eaton, Man. Bot. (ed. 6) 29 (1833).

Aronia botryapium var. *β racemosa* Persoon, l.c.

Aronia ovalis sensu Elliott, Sketch Bot. S.C. & Ga. 1:558 (1821). Non Persoon 1807.

Pyrus ovalis sensu Bigelow, Fl. Boston. (ed. 2) 195 (1824). Non Willdenow, 1796, nec *Amelanchier ovalis* Medicus 1793, nec Borkhausen 1803.

Amelanchier intermedia Spach, Hist. Nat. Vég. Phan. 2:85 (1834); M. Roemer, Syn. Mon. 3:146 (1847); Blanchard in Torreya 7:98 (1907) ex p.; Britton & Shafer, N. Am. Tr. 438, fig. 384 (1908); Stone, Pl. So. N.J. in Rep. N.J. State Mus. 1910:488 (1911); Britton & Brown, Illustr. Fl. N. U.S. (ed. 2) 2:292, fig. 2330 (1913); Wiegand in Rhodora 22:147 (1920); Hoffmann in Proc. Boston Soc. Nat. Hist. 36:280 (1922); House in N.Y. State Mus. Bull. 254:412 (1924); Wiegand & Eames, Fl. Cayuga Basin 248 (1926); Rehder, Man. Cult. Tr. & Shr. 390 (1927).

Mespilus glabra Nuttall ex Hooker, Fl. Bor. Am. 1:202 (1834).

Pyrus neumanniana Tausch in Flora 21:76 (1838).

Aronia affinis Neum. ex Tausch, ibid.

Amelanchier canadensis var. β *oblongifolia* Torrey & Gray, Fl. N. Am. 1:473 (1840); Torrey, Fl. N.Y. 1:225 (1843); Walpers, Rep. Bot. Syst. 2:55 (1843); Gray, Man. Bot. 130 (1848), (ed. 2) 126 (1856); Watson & Coulter in Gray, Man. Bot. (ed. 6) 167 (1889).

Amelanchier ovalis sensu Emerson, Tr. Massachusetts 444 (1846). Non Medicus 1793.

Amelanchier oblongifolia M. Roemer, Syn. Mon. 3:147 (1847); Robinson & Fernald in Gray, New Man. Bot. (ed. 7) 460 (1908); Jones & Rand in Bull. Vermont Agr. Exp. Sta. 145:99 (1909); Wiegand in Rhodora 14:147, pl. 96 (1912); Clements, Rosendahl, & Butters, Minnesota Tr. & Shr. 151 (1912); Small, Florida Tr. 31 (1913), Shr. of Florida 29 (1913); Small & Carter, Fl. Lancaster Co. Pennsylvania 155 (1913); Bean, Tr. & Shr. Brit. Isles 1:189 (1914); Rehder in Bailey, Stand. Cyclop. Hort. 273 (1914); Hitchcock & Standley, Fl. Distr. Columbia 178 (1919); Silva Tarouca, Freiland-Laubh. (ed. 2) 96, fig. 86 (1922); Bailey, Man. Cult. Pl. 378 (1924); Rehder, Man. Cult. Tr. & Shr. 389 (1927); Rydberg, Fl. Prairies & Plains 437 (1932); Small, Man. Se. Fl. 636 (1933); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 388 (1940).

Amelanchier neumanniana M. Roem., l.c.

Amelanchier spicata sensu Decaisne in Nouv. Arch. Mus. Hist. Nat. Paris 10:135, pl. 9 (1874). Non *Crataegus spicata* Lam.

Amelanchier canadensis var. *obovalis* Britton, Stern, & Poggenberg, Prelim. Cat. 17 (1888) excl. syn.; Sargent, Silva N. Am. 4:128, pl. 195 (1892), pro maxime parte; Dippel, Handb. Laubh. 3:392 (1893); Schneider, Illustr. Handb. Laubh. 1:734, figs. 409, 410 (1906); Silva Tarouca, Freiland-Laubh. 139, fig. 124 (1913).

Amelanchier nantucketensis Bicknell in Bull. Torr. Club 38:453 (1911).

Amelanchier canadensis intermedia Ashe in Bull. Torr. Club 46:221 (1919).

Amelanchier sera Ashe in op. cit. 222; Rehder, Man. Cult. Tr. & Shr. 390 (1927), (ed. 2) 388 (1940).

Amelanchier oblongifera Ashe, l.c. (err. in transcr.).

Amelanchier longifolia Stapf in Index Lond. 1:116 (1929) (err. in transcr.).

Amelanchier austromontana sensu Fernald in Rhodora 43:566 (1941), ex p. Non Ashe 1918.

Shrub 2-8 m. tall, the stems slender, erect, fastigiately branched, forming close bushy clumps; bark of the twigs grayish, glabrous; winter buds small, dark brown, glabrous or nearly so; leaves thin, usually nearly exactly elliptical, varying to oval or narrowly obovate, conduplicate in the bud, unfolding at flowering time, the lower surface densely white-tomentose, soon glabrous throughout, or the midvein and petiole often remaining slightly pubescent; blades mostly 3.5-5 cm. long, 1.5-2.5 cm. wide, acutish, or rounded and mucronate at the apex, the base rounded, rarely subcordate or cuneate; lateral veins 9-13 pairs, irregularly and distantly arranged, usually curved upward toward the middle and becoming irregular and indistinct before reaching the margin; margins sharply serrate with low sharp teeth, the lower part of the blade nearly or quite entire; teeth 6-11 per cm., 25-40 on each margin on average leaves; petioles slender, 8-15 mm. long; flowers small, appearing with the leaves; racemes erect 2.5-6 cm. long, the rachis and pedicels whitish pubescent at first, the lower pedicels 5-10 mm. long; petals 5, white, oval or oblanceo-

late, obtuse, 3-9 mm. long, 2-3 mm. broad; stamens about 20, the fila-
ments glabrous, 2-4 mm. long; anthers 1 mm. long; hypanthium campanu-
late, 3-5 mm. in diameter, tomentulose at the base or throughout, scarcely
constricted on the fruit; sepals triangular-lanceolate, 1.5-2.5 mm. long,
pilosulous within, mostly erect or ascending on the fruit; styles 5,
glabrous, 4-5 mm. long, fused to near the middle; summit of ovary
glabrous or nearly so; fruit globose or subglobose, 7-10 mm. in diameter,
purplish black, glaucous, sweet, juicy, edible; lowest fruiting pedicels 1-2
cm. long; seeds brown, smooth, obliquely lanceoloid, 4-5 mm. long, 2-3
mm. wide.

Type Locality: "Habitat in Virginia, Canada." Phototypes in the
Gray Herbarium and in the herbarium of the Arnold Arboretum. Type in
the Linnean Herbarium.

Range: A species chiefly of swamps and bogs, and in low ground in
woods, from Newfoundland to Georgia, principally on the Coastal Plain.
Flowering from the end of March to the latter part of May; fruit ripen-
ing in June and July. Common names: shadbush, thicket shadblow,
wild pear.

Newfoundland: Topsail Road, July 1931, *Ayre* (GH); Salmonier Line,
Knowlting in 1928 (GH).

New Brunswick: Grand Manan, *Weatherby* 7029 (GH); Bass River, June 2,
1869, *Fowler* (GH).

Nova Scotia: Bridgewater, *Fernald & Long* 23946 (GH); Dartmouth, *Jack*
684 (AA); Barrington, *Fernald, Long, & Linder* 21456 (GH); Maccan, *Jack* 3583
(AA); Truro, *Jack* 3639 (AA); Port Mouton, *Bissell & Graves* 21457 (GH);
Ohio, *Jack* 3108 (AA); Yarmouth, *Bissell, Pease, Long, & Linder* 21440 (GH);
Arcadia, *Pease & Long* 21453 (GH); Goven Lake, *Fernald, Bartram, & Long*
23937 (GH).

Prince Edward Island: Bothwell, *Fernald & St. John* 11085 (GH).

Maine: Orono, May 1898, *Harvey* (UI); Waldo Co., *Hyland* 699 (GH); Jones-
port, *Hyland* 753 (GH); Stillwater, May 12, 1896, *Merrill* (NE); South Poland,
Furbish in 1893 (NE); Gilead, *Furbish* in 1897 (NE); Brunswick, *Furbish* in 1892
(NE); West Baldwin, *Furbish* in 1900 (NE); North Berwick, May 9, 1897,
Fernald (NE); Trotts Island, May 22, 1895, *Fernald* (NE); Alfred, *Fernald &
Long* 13772 (AA, NE); York, *Bicknell* 4840 (NE); Wells, *Furbish* in 1898 (NE).

New Hampshire: Wolfeboro, *Sargent* 21 (GH); Winchester, May 11, 1912,
Flint (NE); Andover, *Jack* 3948 (AA); Dover, *Hodgdon* 2597 (NE); Barrington,
Hodgdon 2773 (NE); Merrimac Co., July 14, 1933, *Bullard* (NE); Bennington,
June 29, 1908, *Coville* (AA); Epping, *Pease* 24229 (NE); Derry, May 10, 1913,
Batchelder (NE); Charlestown, *Woodward & Bean* 17116 (NE).

Vermont: Westminster, May 14, 1902, *Blanchard* (GH); Bellows Falls, May
10, 1915, *Knowlton* (NE).

Massachusetts: Plymouth, *Fernald & Hunnewell* 15200 (NE); Nantucket
Island, *Bicknell* 4815, 4847, 4851, 4858, 4862a, 4868, 4879 (NY), 4816, 4850 TYPE
collection of *A. nantucketensis* (NY, NE), 4849 (NY, GH), 4857 (NE),
Day 57 (NY), 75 (NY, GH, NE); Lexington, *Kennedy* 3260 (NE); Concord,
Kennedy 2360 (GH); Amherst, *Seymour* 3493 (NE); Salem, July 4, 1925, *Mackin-
tosh* (NE); Chicopee, *Seymour* 571 (GH); Wellesley, *Wiegand* 2131, 2132 (GH);
Blue Hill, Milton, *Palmer* 20185 (AA); Harwich, *Fernald & Long* 18542 (NE);
Haverhill, *Harris* 423 (NE); Yarmouth, June 1916, *Winslow & Sanford* (NE);

Brewster, *Fernald* 18546 (GH, NE); Barnstable, *Fernald & Long* 16869, 18543 (NE); West Tisbury, *Seymour* 1222 (GH, NE); Revere, June 28, 1882, *Young* (NE); New Bedford, May 7, 1910, *Hervey* (NE); Mt. Wachusett, May 11, 1897, *Bailey* (NE); Douglas, *Fernald* 15191, 15198, 15199 (NE); Lunenburg, *Fernald & Bean* 14160 (NE); Leicester, *Hunnewell & Wiegand* 2137, 2139, 2140, 2143 (NE).

CONNECTICUT: Coventry, *Weatherby* in 1935, Pl. Exsicc. Gray. 662 (GH); Franklin, *Woodward* in 1915 (NE); East Putnam, June 10, 1922, *Eaton & Fassett* (NE); Southington, *Bissell* in 1901 (GH, NE); Waterford, *Graves* in 1901 (GH); Middlebury, July 4, 1910, *Blewitt* (GH); Kent, *Weatherby* 4916 (NE); New Haven, Apr. 26, 1878, *Allen* (NE); Waterbury, *Blewitt* 1508, 1801 (NE).

RHODE ISLAND: Warwick, Apr. 17, 1910, *Hope* (NE); Barrington, May 30, 1911, *Winslow* (NE); Charlestown, *Collins* in 1919 (NE); South Kingston, *Gilbert, Rehder, & Smith* 833 (NE); East Providence, *Wiegand* 991 (NE); Block Island, *Fernald & Long* 9625 (GH, NE); Little Compton, July 27, 1919, *Collins* (NE).

NEW YORK: Niagara Falls, July 8, 1898, *Schneck* (UI); Waterloo, *Wiegand* 2541 (GH); Oneida Lake, *Muenscher & Spalteholz* 16175 (GH); Oswego, *Wiegand* 15627 (GH); Preble, *Wiegand* 2539 (GH); Glens Falls, *Burnham* 11 (GH); Round Marsh, *Dudley* 56 (GH); Peekskill, *McKelvey* in 1933 (AA); Brooklyn, May 1, 1886, *Stabler* (GH); Ithaca, *Wiegand & Eames* 2515, 2517, 2518 (GH).

MAP 6.—Range of *Amelanchier canadensis.*

NEW JERSEY: Riverton, Apr. 29, 1879, *Eisele* (AA); Millville, *Adams* 339 (GH); Merchantville, *St. John & Long* 1063 (GH); Lakewood, *Byhouwer & Kobuski* 50 (AA); Egg Harbor City, *Hunnewell* 6031 (GH); Hammonton, May 27, 1923, *Bassett* (GH); Medford, *Long* 26820 (GH); Forked River, *Moldenke* 10580 (UI); Lakehurst, May 15, 1910, *Mackenzie* (GH); Island Heights, *Muenscher* 50 (GH).

PENNSYLVANIA: Philadelphia, May 1, 1926, *McDowell* (GH); Franklin Co., *Jennings* 1581 (GH); Brandamore, July 26, 1925, *Stone* (GH); Folsom, *Long* 58240 (Ph); Tinicum, *Stone* 6484 (Ph); Morrisville, *Long* 34224 (Ph); Bacton, *Long* 31233 (Ph); Harmonyville, *Long* 33309, 33615 (Ph); Nottingham, *Long* 33330 (Ph); Fontaine, *Long* 32689 (Ph).

DELAWARE: Vandyke, *Tidestrom* 11947 (GH); Townsend, April 8, 1909, *Long* (Ph); Wilmington, *A. Commons* in 1875 (Ph).

DISTRICT OF COLUMBIA: North Takoma, May 2, 1897, *Williams* (AA); Naucks, June 1, 1913, *Steele* (AA).

MARYLAND: Elkton, *Wherry & Adams* 2775 (GH); Lanham, *Blake* 9324 (GH); Riggs Mill, Prince Georges Co., *Blake* 9362 (GH); Bacon Hill, *Long* 57005 (Ph); North East, *Long* 57021 (Ph); Principio Furnace, *Long* 54350 (Ph).

WEST VIRGINIA: Roland Park, Gabell Co., *Gilbert* 398 (GH).

VIRGINIA: Accomac, *Pease* 26992 (GH); Falmouth, *Wiegand & Manning* 1328 (GH); Richmond, April 13, 1887, *Kennedy* (GH); Clarendon, *Allard* 1229 (GH); Williamsburg, *Menzel* 403 (GH); Sebrell, *Fernald & Long* 7869 (GH, Ph); Franklin, *Fernald & Long* 9949, 11343 (GH, Ph); Lee's Mill, *Fernald & Long* 12096 (GH, Ph); Zuni, *Fernald & Long* 7068 (GH); Emporia, *Fernald & Long* 7070 (GH, Ph); Little Texas, *Fernald, Long, & Pease* 11700 (GH, Ph).

NORTH CAROLINA: Abbottsburg, *Harbison* 8 (AA); Pleasant Hill, *Fernald & Long* 7071 (GH, Ph); Hamlet, *Wiegand & Manning* 1330 (GH); Blount Creek, *Godfrey, White, & Shelbourne* 7038 (GH, MBG); Lumberton, *Wiegand & Manning* 1331 (GH).

SOUTH CAROLINA: Sumter, *Rehder* 955 (AA); Seneca, *Palmer* 35412 (MBG); Manning, *Stone* 65 (Ph).

GEORGIA: Augusta, *Sargent* in 1900 (AA); Graymont, *Harper* 819 (GH); Franklin, *Hermann* 10048 (GH).

In the flowering stage, this species may be recognized by the glabrous ovary, short petals, and the erect tomentose-lanate racemes; the densely pubescent leaves are about half unfolded. In the fruiting stage the rather firm elliptical or slightly obovate finely serrate leaves that are soon quite glabrous, dark green, smooth, and somewhat glossy above, paler beneath, with rounded base and acutish or rounded, often mucronulate apex, are distinctive. This species is apparently closely related to *A. spicata,* from which it usually may be distinguished by the somewhat different habit of growth, the elliptical leaves, glabrous top of the ovary, and the somewhat larger fruits, with erect or spreading sepals.

A peculiarity of *A. canadensis* has been well described by Wiegand (Rhodora 14:149. 1912): "As the fruit matures the inflorescence expands much less in this species than in others, the axis and pedicels remaining short. The shoots upon which the racemes are borne remain short also, while frequently there is a strong growth of leafy shoot beyond the inflorescence and as a result the inflorescence often appears to have been left far behind, and to have been lateral when really terminal. Unfortunately this condition is too frequently obscure to be of use as a distinguishing characteristic."

For some reason not apparent, the younger Linnaeus, when transferring his father's *Mespilus canadensis* to the genus Pyrus, gave it a new specific name, *botryapium.* However, the earliest name that applies to this species is clearly *Mespilus canadensis* L., which was transferred to Amelanchier by Medicus in 1793. In his discussion of certain eastern North American species of Amelanchier, Fernald (Rhodora 43:560-561. 1941) observes: "*Mespilus canadensis* L. Sp. Pl. 1:478. 1753 was published with unusual lack of involving references, merely the plant of Linnaeus's herbarium described, with a single reference to a description of Gronovius. . . . It is, therefore, unfortunate that, when he so clearly differentiated our species of Amelanchier and thus gave study to the genus a new and stimulating interest, Wiegand seems to have misunderstood the

basis of *A. canadensis*. He had had a comparison made by a botanist not
familiar with the eastern species and he then used the Linnean name for
the largest member of the genus, the large shrub or tree with cordate,
ovate, or broadly ovate-oblong, sharply serrate leaves which, like those
of true *A. canadensis* (*A. oblongifolia*), are pubescent beneath on unfold-
ing, losing most of their pubescence with age." This is the species now
called *A. arborea* (Michx.f.) Fern. For a more extended discussion of
the nomenclatural history of *A. canadensis* (L.) Medic., the reader should
consult the article just quoted.

Pyrus neumanniana Tausch, based on material growing in the Leibnitz
garden at Prag, is represented by a sheet in the Bernhardi Herbarium at
the Missouri Botanical Garden. This sheet is probably part of the original
Tausch exsiccatae and may therefore be regarded as authentic. Wiegand,
in 1912, labeled it "a probable hybrid" with *A. bartramiana* (Tausch)
M. Roem. as one of the parents. Later the sheet was annotated in pencil
by Professor Alfred Rehder: "*A. Botryapium* Borkh." It contains two
specimens, a fruiting branch and a flowering one. The leaves are those
of typical *A. canadensis* (L.) Medic., and match perfectly those of a
photograph of the Linnean type. The small flowers, as well as the rather
characteristic inflorescence, belong unmistakably to *A. canadensis*.

The binomial, *A. spicata* Decaisne, 1874, like that of K. Koch five
years earlier, was based on the name *Crataegus spicata* Lam., but it is
clearly evident from Decaisne's description ("vertice ovarii glabris, stylis
coalitis"), as well as from the floral structures shown in the accompanying
plate, and by the cited synonyms (i.e., *A. ovalis* Lindl., *Mespilus ovalis*
Willd., and *M. canadensis β oblongifolia* Torr. & Gray), and the state-
ment of geographical range, that Decaisne was dealing with *A. canadensis*
(L.) Medic. instead of the plant that Lamarck had called *Crataegus
spicata*. Hence, *A. spicata* sensu Dcne. is a synonym of *A. canadensis* (L.)
Medic., not of *A. spicata* (Lam.) K. Koch, as it is sometimes cited.

In 1911, E. P. Bicknell described as *A. nantucketensis* Bickn. a "shrub
1.5 dm. to 2 m. high" with short petals and glabrous ovary. This was said
to be common in low grounds about the borders of swamps on Nantucket
Island, Massachusetts. From an examination of an isotype, it is evident
that Bicknell's plants are a small form of *A. canadensis* (L.) Medic.
This conclusion is supported by the fact that this species is not un-
common on Nantucket, and by Bicknell's statement that "intermediates"
between his plant and *A. canadensis* (L.) Medic. have been found in the
vicinity. It should be noted here that Bicknell's plants are not the same
as those described four years earlier as *A. oblongifolia* var. *micropetala*
by B. L. Robinson. The specimens cited by Robinson are apparently a
small-flowered form of *A. spicata* (Lam.) K. Koch.

It may be worth noting that occasional specimens of *A. canadensis*

bear leaves somewhat resembling those of *A. spicata*. Such conditions are the probable basis for the statement by Robinson & Fernald in Gray's Manual (ed. 7, p. 460) under *A. oblongifolia* (T. & G.) Roem.: "Highly variable, passing into forms with broader elliptical or ovate-lanceolate acutish leaves of deeper green color (being the *A. spicata* of many auth., not C. Koch). Apparently intergrades with other species."

8. AMELANCHIER OBOVALIS (Michx.) Ashe
(Plates VIII, XXII, XXIII)

(?) *Mespilus amelanchier* sensu Walter, Fl. Carol. 148 (1788). Non L. 1753.
Mespilus canadensis var. α *obovalis* Michaux, Fl. Bor. Am. 1:291 (1803).
Amelanchier oblongifolia var. β *walteri* M. Roem. Syn. Mon. 3:147 (1847).
Amelanchier canadensis var. *obovalis* Sargent, Silva N. Am. 4:128 (1892), pro parte, excl. pl. 195.
Amelanchier obovalis Ashe in Bot. Gaz. 35:434 (1903); Sargent, Man. Tr. N. Am. 361, fig. 284 (1905), ex parte; Fernald in Rhodora 43:566, pl. 672, fig. 3 (1941).
Crataegus canadensis obovalis Sargent ex Ashe in l.c. (err. in transcr.)
Amelanchier oblongifolia sensu Wiegand in Rhodora 14:147 (1912), ex parte.
Amelanchier stolonifera Wiegand, in op. cit. 144, ex parte.

Low shrubs 0.2-1.5 m. tall, surculose, and forming loose colonies; winter buds conical, acute, reddish brown, dull, vernicose, the scales ciliate; twigs slender, soon glabrous; leaves commonly oval or elliptical, varying to slightly obovate, conduplicate in the bud, densely whitish tomentose beneath when young, unfolding after the flowers, which are on leafless or nearly leafless twigs; mature blades of rather firm texture, 2-5 cm. long, 1-3 cm. wide, the apex acutish, or obtuse and mucronulate, the base acute or rounded, or less commonly slightly subcordate, the upper surface dark green, dull, or somewhat glossy, smooth, the lateral veins not particularly prominent, the midvein impressed, the lower surface pale green, rather prominently veined, glabrous or nearly so at maturity, or with lingering traces of tomentum; lateral veins 7-9 pairs, irregularly and distantly arranged, usually curved upward and becoming irregular and indistinct before reaching the margin; margins sharply serrulate nearly or quite to the base, or frequently the lower third nearly or quite entire; teeth 6-9 per cm., 20-30 on each side of average leaves; stipules linear, pubescent, soon deciduous; petioles 5-15 mm. long, glabrous or slightly pubescent at maturity; flowers precocious, in short, dense, compact, erect, usually leafless, 4-10-flowered racemes 1-3 cm. long, the lower pedicels 1-3 mm. long; petals 5, white, glabrous, elliptical, minutely clawed, obtuse, 6-7 mm. long, 3-4 mm. wide; stamens 20, the filaments glabrous; anthers 0.6-0.7 mm. long; hypanthium saucer-shaped, 2-3 mm. in diameter, tomentulose outside, not at all constricted on the young fruit; sepals triangular, acute, 1-2 mm. long, pubescent within, divergent after anthesis; styles 5, glabrous, 2-3 mm. long, usually united below the middle; top of the ovary glabrous; mature fruits globose, purplish black, glabrous, 6-8 mm. in diameter, sweet, juicy, edible; fruiting racemes erect, compact; 2-3 cm.

long, 2-8-fruited (average 4); sepals on the fruit erect or divaricate, less commonly somewhat reflexed, glabrous, triangular-lanceolate, 2-3 mm. long; fruiting pedicels usually 3-8 mm. in length, or occasionally the lowest becoming 11 or even 14 mm. long; seeds reddish brown, smooth, obliquely lanceloid, somewhat flattened, obtusish at each end, 4-5 mm. long, 2-2.5 mm. wide.

TYPE LOCALITY: "In Carolina inferiore." Type in Michaux's herbarium in the Museum d'Histoire Naturelle, Paris. Phototype in the Gray Herbarium.

RANGE: Open woods or sandy pine barrens along the Atlantic Coastal Plain, from Pennsylvania to Georgia; flowering in late March and early April; fruits ripening in May and June.

PENNSYLVANIA: Near Slatedale, *Pretz* 8296, 9260 (Ph); Point Pleasant, *Benner* 2703, *Long* 32883 (Ph); Naceville, *Long* 18759 (Ph); Yardley, *Long* 30300 (Ph); Spring House, *Long* 33071 (Ph); Wakefield, *Tanger* 3351 (Ph); Castle Rock, June 9, 1904, *Jahn* (Ph); Folsom, *Long* 58269 (Ph).

NEW JERSEY: Scott's, Middlesex Co., May 28, 1922, *Mackenzie* (Ph); Shark River Station, May 21, 1922, *Mackenzie* (Ph); Clarksburg, *Long* 45720 (Ph); Charleston Springs, *Long* 52012 (Ph); Chatsworth, *Long* 16451 (Ph); Clementon, *Long* 21005 (Ph); Ostrom, *Long* 48766 (Ph); Prospertown, *Long* 30603 (Ph); Friesburg, *Long* 35296 (Ph); Parkdale, *Long & Pennell* 7364, 7374 (Ph); Newtonville, *Long* 5915, 48268 (Ph); Fairview, *Long* 30773 (Ph); East Creek, *Long* 21590 (Ph); Wildwood Junction, *Bartram* 3220 (Ph); Browns Mills, April 30, 1905, *MacElwee* (Ph).

MARYLAND: Elkton, *Long* 54322 (Ph); Bacon Hill, *Long* 54368 (Ph); North East, *Long* 54423 (Ph).

VIRGINIA: McKenney, *Fernald & Long* 13950 (Ph); Petersburg, *Fernald, Long, & Smart* 5790, *Fernald & Long* 9947 (GH, Ph); Waverly, *Fernald & Long* 7072, 7870, 13042 (GH, Ph); Homeville, *Fernald & Long* 7073 (GH, Ph); Franklin, *Fernald & Long* 7448 (GH, Ph); Suffolk, *Fernald & Long* 7074 (GH, Ph); Whaleyville, *Fernald & Long* 7449 (GH, Ph); Lee's Mill, *Fernald & Long* 11846 (GH, Ph); Orion, *Fernald & Long* 13043 (GH, Ph); Emporia, *Fernald & Long* 11847 (GH, Ph).

NORTH CAROLINA: French Broad River, June 1898, *Biltmore Herbarium* 6706 (GH, AA).

SOUTH CAROLINA: Near Charleston, *Hunt* 2969, *Hunt & Martin* 1408, 2526 (UI).

Amelanchier obovalis (Michx.) Ashe is a dwarf surculose shrub, forming loose colonies, with the flowering or fruiting stems only 0.2-1.5 m. high, superficially resembling, but apparently quite distinct from, the widespread *A. spicata* (Lam.) K. Koch. At flowering time it may be distinguished from that species by the precocious flowers in compact racemes on leafless twigs, and by the glabrous ovary. It bears some structural resemblances to *A. canadensis* (L.) Medic, but differs in its smaller size and dissimilar growth-form, as well as the usually more oval leaves, somewhat shorter petals, and the shorter fruiting pedicels.

This species of dwarf shrubs was described by Michaux in 1803 as *Mespilus canadensis*, "Var. *a obovalis*: humilior; foliis oblongiuscule ovalibus . . . in Carolina inferiore." A phototype (Plate VIII, fig. 2)

shows Michaux's original labels *"Mespilus canadensis a obovalis.* Arbriss [eau] de deux pieds de haut. Carolines." Wiegand in 1912 treated it tentatively as a synonym of *A. canadensis* [*oblongifolia*], but it had been raised to specific rank by W. W. Ashe in 1903. After several seasons of field work in southeastern Virginia, Fernald & Long concluded that it is distinct, and in a recently published study (1941) of the flora of Virginia, Fernald has treated these plants as a separate species.

Thomas Walter's *"Mespilus Amelanchier?"* is somewhat doubtfully included here. Miss Nell Horner, Librarian of the Missouri Botanical Garden, kindly supplied the following transcript of the original description: "inermis, foliis ovato-lanceolatis, crenatis, tenellis tomentosis adultioribus laevibus nitidis; floribus corymbosis."

9. AMELANCHIER SPICATA (Lam.) K. Koch
(Plates II, XII, XIII, XIV, XV, XVI)

Crataegus spicata Lamarck, Encycl. Méth. Bot. 1:84 (1783).

Pyrus ovalis Willdenow, Berlin Baumz. 259 (1796), Sp. Pl. 2:1014 (1799), Enum. Pl. 525 (1809); Muhlenberg, Cat. Pl. Am. Sept. 49 (1813); Pursh, Fl. Am. Sept. 340 (1814); Sprengel, Syst. Veg. 2:509 (1825).

Amelanchier ovalis sensu Borkhausen, Theor.-prakt. Handb. Forstbot. 2:1259 (1803); DeCandolle, Prodr. 2:632 (1825); Spach, Hist. Veg. Phan. 2:85 (1834); M. Roemer, Syn. Mon. 3:146 (1847); Dippel, Handb. Laubh. 3:390 (1893); Rehder in Bailey, Stand. Cyclop. Hort. 273 (1914). Non Medicus 1793.

Aronia ovalis Persoon, Syn. Pl. 2:40 (1807); Torrey, Fl. N. Middle U.S. 479 (1824).

Amelanchier spicata (Lam.) K. Koch, Dendrol. 1:182 (1869), as to name only, excl. syn. & descr.; Koehne, Deutsche Dendr. 256 (1893); Britton & Brown, Illustr. Fl. N. U.S. 2:238, fig. 1987 (1897); Britton, Man. Fl. N. States 517 (1901), (ed. 3) 519 (1907); Small, Fl. Se. U.S. 532 (1903); Card in Bailey, Cyclop. Am. Hort. 57 (1904); Schneider, Illustr. Handb. Laubh. 1:737, figs. 411, 412 (1906); Apgar, Ornam. Shr. U.S. 182, fig. 279 (1910); Britton & Brown, Illustr. Fl. N. U.S. (ed. 2) 2:292, fig. 2331 (1913); Rehder, Man. Cult. Tr. & Shr. 389 (1927), (ed. 2) 388 (1940); G. N. Jones, Fl. Illinois 154 (1945).

Amelanchier canadensis var. *spicata* Sargent, Silva N. Am. 4:129 (1892).

Amelanchier saxatilis Blanchard in Torreya 7:99 (1907).

Amelanchier erecta Blanchard, op. cit. 101.

Amelanchier intermedia sensu Blanchard, l.c. Non Spach 1834.

Amelanchier oblongifolia sensu Robinson & Fernald in Gray, Man. Bot. (ed. 7) 460 (1908), ex p. Non M. Roem. 1847.

Amelanchier oblongifolia var. *micropetala* Robinson in Rhodora 10:33 (1908); Robinson & Fernald in Gray, New Man. Bot. (ed. 7) 460 (1908); Rehder, Man. Cult. Tr. & Shr. 389 (1927), (ed. 2) 388 (1940).

Amelanchier humilis Wiegand in Rhodora 14:141, pl. 95 (1912); Clements, Rosendahl, & Butters, Minnesota Tr. & Shr. 153 (1912); Rehder in Bailey, Stand. Cyclop. Hort. 272 (1914); Rydberg, Fl. Rocky Mts. 447. (1917); House, N.Y. State Mus. Bull. 254, 413 (1924); Deam, Shr. of Indiana 145, pl. 58 (1924); Wiegand & Eames, Fl. Cayuga Basin 247 (1926); Rehder, Man. Cult. Tr. & Shr. 389 (1927); Rosendahl & Butters, Tr. & Shr. Minnesota 216 (1928); Peattie, Fl. Indiana Dunes 219 (1930); Palmer & Steyermark in Ann. Missouri Bot. Gard. 22:557 (1935); Marie-Victorin, Fl. Laurent. 316, fig. 91 (1935); Nielsen in Am. Midl. Nat. 22:171, pls. 5-8 (1939) (excl. syn.); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 387 (1940); Steyermark, Spr. Fl. Missouri 255, pl. 68, fig. 2 (1940); Deam, Fl. Indiana 532 (1940).

Amelanchier stolonifera Wiegand in Rhodora 14:144, pl. 95 (1912), ex p.; Small &
  Carter, Fl. Lancaster Co., Pa. 155 (1913); Rehder in Bailey, Stand. Cyclop.
  Hort. 273 (1914); Hitchcock & Standley, Fl. Distr. Columbia 178 (1919); Hoff-
  mann in Proc. Bost. Soc. Nat. Hist. 36:281 (1922); Pease in ibid. 37:267 (1924);
  House in N.Y. State Mus. Bull. 254:412 (1924); Wiegand & Eames, Fl. Cayuga
  Basin 247 (1926); Rehder, Man. Cult. Tr. & Shr. 389 (1927); Rosendahl &
  Butters, Tr. & Shr. Minnesota 219 (1928); Small, Se. Fl. 636 (1933); Marie-
  Victorin, Fl. Laurent. 316, fig. 91 (1935); Nielsen in Am. Midl. Nat. 22:177,
  pl. 2, b (1939); Rehder, Man. Cult. Tr. & Shr. 387 (1940).
Amelancus spicata Vollman, Fl. Bayern 453 (1914).
Amelanchier botryapium var. *obovalis* Farwell in Rep. Mich. Acad. Sci. 17:175
  (1916).
Amelanchier botryapium var. *conferta* Farwell, l.c.
Amelanchier botryapium var. *micropetala* Farwell in op. cit. 176.
Amelanchier austromontana Ashe in Journ. Elisha Mitchell Sci. Soc. 34:138 (1918).
Amelanchier beata Ashe, l.c.
Amelanchier micropetala Ashe in Bull. Torr. Club 46:223 (1919).
Amelanchier micropetala var. *potomacensis* Ashe, l.c.
Amelanchier stolonifera var. *lucida* Fernald in Rhodora 23:267 (1922).
Amelanchier humilis var. *typica* Nielsen in Am. Midl. Nat. 22:171, pl. 5 (1939).
Amelanchier humilis var. *compacta* Nielsen, op. cit. 174, pl. 7.
Amelanchier humilis var. *campestris* Nielsen, op. cit. 176, pl. 6.
Amelanchier humilis var. *exserrata* Nielsen, op. cit. 177, pl. 8.
Amelanchier mucronata Nielsen, op. cit. 178, pl. 9.
Amelanchier humilis × *laevis* Deam, Fl. Indiana 532 (1940).
Amelanchier canadensis var. *micropetala* Rehder in Journ. Arnold Arb. 26:71 (1945).

Low, surculose colonial shrubs 0.3-2 m. tall; winter buds conical, acute,
reddish brown, dull, vernicose, the scales ciliate; leaves commonly oval,
varying to broadly ovate or suborbicular, conduplicate in the bud, unfold-
ing before or with the flowers and usually about half-grown at anthesis
(rarely the flowers on nearly leafless twigs), densely whitish tomentose
beneath when young; mature blades 2.5-5 cm. long, 2-3.5 cm. wide, the
apex acutish, or obtuse and more or less mucronate, the base rounded or
less commonly subcordate, usually nearly or quite glabrous on both sur-
faces; lateral veins 7-9 pairs, not prominent, irregularly and distantly
arranged, usually curved upward and becoming irregular and indistinct
before reaching the margin; margins finely and evenly serrate nearly or
quite to the base, or frequently the lower third almost or quite entire; teeth
5-8 per cm., 20-30 on each side of average leaves; stipules linear, pubescent,
deciduous; petioles slender, 1-2 cm. long, glabrous or slightly pubescent
at maturity; flowers in short, dense, erect, 4-10-flowered racemes 1.5-4
cm. long, the lower pedicels 6-18 mm. long; petals 5, white, or sometimes
pinkish, oblanceolate, obtuse, 4-10 mm. long, 3-4 mm. wide; stamens about
20, the filaments glabrous; anthers 0.6-0.9 mm. long; hypanthium saucer-
shaped, 3-4 mm. in diameter, glabrous or pubescent outside, more or less
constricted on the young fruit; sepals triangular-lanceolate, acute, 2-3 mm.
long, pubescent within, usually recurved from the middle after anthesis;
styles 5, glabrous, 2-3 mm. long, usually united only near the base; top of

the ovary densely tomentose; mature fruit globose, purplish black, glaucous, glabrous, 6-8 mm. in diameter, sweet, juicy, edible; lower pedicels 1-3 cm. long; seeds brown, smooth, obliquely lanceoloid, somewhat flattened, about 5 mm. long, 2-3 mm. wide when well developed.

TYPE LOCALITY: Cultivated in the Jardin du Roi, Paris; said to have come originally from Canada. Phototype and fragment of holotype in the herbarium of the Arnold Arboretum. Type in the Museum d'Histoire Naturelle, Paris.

RANGE: On gravelly or rocky shores or river banks, sandstone or limestone cliffs and ledges, rocky summits, in woods or thickets, pine barrens, or sand dunes, from Newfoundland to Alabama, eastward to Missouri and Minnesota (and eastern North Dakota). Flowering from the beginning of April in the south to the middle of June (or somewhat later) in the northern part of its range; fruit ripening from July to September. Common names; low juneberry or shadblow.

NEWFOUNDLAND: Grand Falls, *Fernald & Wiegand* 5557 (GH), 5558 (AA, GH), 5559, 5561, 5562, 5563, 5605, 5608, 5623 (GH), 5633 (GH, AA); Rushy Pond, *Fernald & Wiegand* 5627, 5630, 5635 (GH); Birchy Pond Stream, *Fernald & Wiegand* 3553 (GH); Dildo Run, *Fernald & Wiegand* 5565 (GH); St. Johns, *Ayre* in 1932 (GH); Trepassy, *Fernald, Long, & Dunbar* 26759 (GH).

NOVA SCOTIA: Middleton, *Fernald, Pease, & Long* 21436 (GH), 21437 (GH, TYPE of *A. stolonifera* var. *lucida,* AA), 21435 (GH, AA), *Jack* 3209 (AA); Port Mouton, *Jack* 3479 (AA); Argyle, *Fernald & White* 21438 (GH), *Pease & Long* 21452 (GH, AA); Kemptville, *Fernald & Long* 23933 (GH); Goven Lake, *Fernald, Bartram, & Long* 23930 (GH); Gavelton, *Fernald, et al.* 23929 (GH); Tusket, *Jack* 3357 (GH, AA), 3762 (AA); Birchtown Brook, *Fernald & Long* 23934 (GH); Barrington, *Fernald, Long, & Linder* 21439 (GH); Springhill Junction, *Pease & Long* 21434 (GH); Shubenacadie Grand Lake, *Fernald, Bartram, & Long* 23931 (AA, GH), *Fernald & Bissell* 21433 (GH); Avonport, *Roland* 2047 (GH); Millville, *Roland* 41469 (GH); Bridgewater, *Fernald & Long* 23932 (GH), *Fernald, et al.* 21432 (GH), *Jack* 3514 (AA).

PRINCE EDWARD ISLAND: Dundee, *Fernald, Long, & St. John* 7593 (GH); Southport, *Fernald & St. John* 7585 (GH); Mt. Stewart, *Fernald, et al.* 7582, 7591, 7553 (GH); Charlottetown, *Fernald & St. John* 11080 (GH); Cavendish, *Fernald, Long, & St. John* 7595 (GH); Indian River, *Fernald, Long, & St. John* 7594 (GH); Tignish, *Fernald, Long, & St. John* 7584 (GH).

NEW BRUNSWICK: Boiestown, *Fernald & Pease* 25134 (GH); Portage Island, *Blake* 5677 (GH); Gorge of the Aroostock River, *Fernald* 1881 (GH); Woodstock, *Fernald & Long* 13781 (GH).

QUEBEC: Montmorency Falls, *Macoun* 66924 (GH); Lake Temiscaming, *M.-Victorin* 8237 (AA); Contrecoeur, *M.-Victorin & R.-Germain* 33110 (AA, GH); Longueuil, *M.-Victorin* 9504, 11221, 11223 (AA); North Wakefield, *Macoun* 85506 (AA); Oka, *M.-Victorin* 24545, 2087 (AA); La Trappe, *M.-Victorin & R.-Germain* 33130 (AA, GH), *Louis-Marie* 116 (GH); Deschenes, *Rolland* 13033, 13035 (GH); Windsor, July 25, 1923, *Knowlton* (GH).

MAINE: Ft. Fairfield, *Fernald* 1888 (NE); Clifton, *Fernald* 2644 (NE); Winn, *Fernald & Long* 13762 (AA, NE); Milford, *Fernald* 13760, 13773, 13774 (NE), 13775 (GH); Dover, *G. B. Fernald* 43 (NE); Fairfield, *Fernald & Long* 13766 (NE); Skowhegan, *Chamberlain* in 1903 (NE); Bald Mt., *Chamberlain & Knowlton* in 1902 (NE); Phillips, *Furbish* in 1894 (NE); Oxford, *Weatherby* in 1914 (NE); Whitneyville, *Knowlton* in 1908 (NE); Mt. Desert I., *Fernald* in 1892
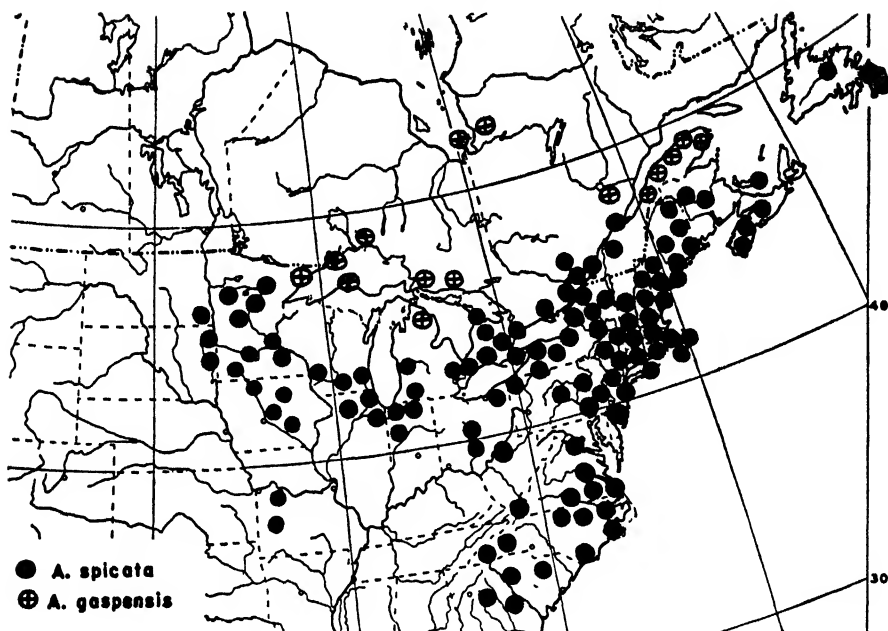
MAP 7.—Range of *Amelanchier spicata* and *A. gaspensis*.

(NE, GH), *Williams* in 1899 (NE), *Rehder* in 1936 (AA); Isle au Haut, *Hill* 1700 (NE); Matinicus, *Long* 320, 335 (NE); Rockland, *Long* 852 (NE); Rockport, *Fernald* 9620 (NE); West Bath, *Furbish* in 1892 (NE); Standish, *Fernald & Long* 13777 (AA, NE); Brunswick, *Chamberlain* 228 (NE); Kennebunkport, *Koehler* 1 (GH); York, *Fernald* in 1900 (GH, NE).

VERMONT: Essex Junction, *Eggleston* 1176 (GH); Burlington, *Blake* 2496 (NE); Barnet, May 31, 1881, *Blanchard* (NE); Snake Mt., near Weybridge, *Brainerd* in 1878 and 1898 (GH); Rutland, *Eggleston* 1179, 1180 (AA, NE, GH, UI); Twin Mts., *Eggleston* 185 (GH); Arlington, *Schweinfurth, et al.* in 1935 (NE); Bellows Falls, *Blanchard* 3 (AA, GH, TYPE coll. of *A. saxatilis*), *Blanchard* 4 (TYPE coll. of *A. erecta,* GH); Westminster, *Blanchard* 4 (GH, AA); North Westminster, *Blanchard* 4 (AA, GH).

NEW HAMPSHIRE: Salem, May 22, 1909, *Churchill & Purdie* (NE, GH); Rindge, May 31, 1913, *Batchelder* (NE); Jaffrey, *Rand & Robinson* 618 (GH); Walpole, *Fernald* 105 (GH), 72 (NE, GH), *Bean & Fernald* 17013, 17014 (NE); New Hampton, *Pease* 25912 (NE); Alton, *Pease* 25775 (NE); Gilford, *Pease* 26541 (NE); Strafford, *Pease* 24246 (NE); Rollinsford, *Hodgdon* 3192 (NE); Dover, *Hodgdon* 2600 (NE); Durham, *Hodgdon* 2845 (NE); Bradford, *Fernald & Svenson* 914 (NE); Franklin, *Jack* 3872 (AA); Andover, *Jack* 3946 (AA); Shelburne, *Pease* 25979 (NE); Lake Umbagog, *Pease* 16554 (NE); Errol, *Pease* 16990 (NE); Ashland, *Fernald* 15197 (GH, NE), 15204 (NE); Bath, *Pease* 19680 (NE); Madison, *Pease* 17890 (NE); Ossipee Lake, *Weatherby & Smith* (Pl. Exsicc. Gray 842) (GH, UI).

MASSACHUSETTS: Washington, May 31, 1909, *Hoffmann* (NE); Lenox, May 27, 1920, *Hoffmann* ,(NE); West Stockbridge, May 23, 1920, *Hoffmann* (NE); Gt. Barrington, June 21, 1915, *Hoffmann* (NE)'; Sheffield, Aug. 27, 1902, July 25, 1912, *Hoffmann* (NE); Montague, May 13, 1911, *Fernald* (NE, GH); Sunderland, *Manning & Seymour* 3687 (NE); Shutesbury, *Tower & Seymour* 3668, 3671 (NE); Agawam, *Weatherby* 4255 (NE); Amherst, *Seymour* 3512 (NE); Northampton, *Goodale & Markert* 76864 (NE); Mt. Holyoke, *Hubbard & Torrey* T352

(NE); Russell, *Fernald* 9626 (NE); Chicopee, *Murdoch & Torrey* T391 (NE); Lunenburg, *Fernald & Bean* 14132 (NE); Athol, June 19, 1935, *Churchill* (NE); Ashburnham, May 19, 1924, *Knowlton* (NE); Holden, *Blake & Fernald* 3645 (NE); Princeton, *R. H. Piper* 76881 (NE); Southbridge, May 19, 1916, *Woodward* (NE); Gloucester, *St. John* 11887 (NE); Andover, *Pease* 683 (NE); Sherborn, *Loomis* 856 (NE); Tyngsboro, *Pease* 23232 (NE); Wellesley, *Wiegand* 2133 (GH, TYPE of *A. stolonifera*); Blue Hill, Milton, June 10, 1900, *Williams* (GH), *Floyd* 801, 803, 980, 1008 (NE), May 11, 1903, and Sept. 22, 1900, *Rehder* (UI), May 7, 1899, *Kennedy & Fernald* (GH, TYPE of *A. oblongifolia* var. *micropetala*), May 6, 1899, *Churchill* (GH, NE), *Bartlett* 846 (GH, UI); Mattapan, May 6, 1905, *Cheever* (NE); Plymouth, *Sanford* 626 (NE); Chilmark, *Seymour* 1708, 1709 (GH); West Tisbury, *Seymour* 4641 (NE); Harwich, *Fernald* 16867 (NE); Barnstable, *Woodward & Fernald* 15202 (NE); Sandwich, *Fernald & Long* 18548 (NE); Yarmouth, *Fernald & Long* 18551 (NE); Provincetown, *Greenman* 3024 (GH), *Fernald &. Long* 18549 (AA, NE).

CONNECTICUT: Salisbury, *Blewitt* 2037 (NE), *Weatherby* 4070, 4070a, 4070b (NE); Sharon, *Weatherby* 3616 (NE); East Hartford, *Weatherby* 2018 (GH); Suffield, *Weatherby* 5370 (NE); Stafford, *Weatherby* D2103 (NE); Hamden, *Blewitt* 1796 (NE); Meriden, *Blewitt* 1795 (NE); Waterbury, *Blewitt* 1511, 1792, 1794 (NE); West Cheshire, *Blewitt* 2035 (NE).

RHODE ISLAND: Barrington, May 30, 1911, *Winslow* (AA, NE); South Foster, June 10, 1922, *Eaton & Fassett* (NE); Cumberland, *Chamberlain* 62 (NE).

NEW YORK: Stockholm, *Phelps* 1585 (GH); Canton, *Phelps* 1583, 1586 (GH); Clare, *Phelps* 1584 (GH); Newcomb, *House* 7265 (GH); Watertown, *House* 8943 (GH); Forestport, *Muenscher & Maguire* 2322 (GH); Ledyard, *Wiegand* 6594 (MBG), 6603, 6587, 6593 (GH); Leroy, *Hill* 231895 (UI); Junius, *Eames & Mac-Daniels* 4285 (GH); McKenney's, Tompkins Co., May 1895, *Wiegand* (GH, TYPE of *A. humilis*); Long Lake, *House* 10175 (GH); Hudson Falls, *Burnham* in 1897 (GH); Sand Lake, *Wiegand* 4290 (GH); Glenmont, *House* 17246 (MBG); Ronkonkoma, July 5, 1908, *Harper* (GH); Babylon, *Svenson* 8012 (GH, MBG); Black Rock Forest, *Raup* 8094 (GH); Cahoonzie, *Muenscher, et al.* 15609 (GH); Sullivan Hill, Chimung Co., *Lucy* 818b (GH); Monroe Co., *Slavin* 203 (AA).

NEW JERSEY: Newport, June 2, 1894, *Dill* (AA); High Point, *Mackenzie* 4201 (GH); Chatsworth, *Eames* in 1894 (GH); Crowfoot, *Fogg* 4049 (GH, Ph); Charlotteburg, *Mackenzie* 3080 (GH); Elm, *Fogg* 1863 (Ph); Clementon, *Long* 20586 (Ph); Robbinsville, *Long* 51838 (Ph); Friesburg, *Long* 37315 (Ph); Mays Landing, *Pennell* 12027 (Ph); Jacksons Mills, *Long* 52088, 52094 (Ph); Cookstown, *Long* 30640 (Ph); Atsion, *Long* 25839 (Ph); New Gretna, *Long* 12504 (Ph); Holmeson, *Long* 52017, 52022 (Ph); Farmingdale, *Stone* 12684, *Brown* 216 (Ph); Spring Valley, *Long* 56467 (Ph).

PENNSYLVANIA: Wilkes Barre, *Palmer* 36296 (MBG); Easton, *Porter* in 1897 (GH); Fleetwood, *Long* 12556 (GH); Fairview, *Wahl* 47 (GH); State College, *Wahl* 33, 73 (GH); Almont, July 18, 1923, *Pretz* (GH); Point Pleasant, *Benner* in 1926 (GH); Beaver Meadows, *Fogg* 16324 (GH); Danielsville, *Long* 48649 (Ph); North Bangor, *Long* 51076 (Ph); Shimerville, *Pretz* 11248 (Ph); Schnecksville, *Pretz* 12754 (Ph); Crackersport, *Pretz* 10767 (Ph); Germansville, *Pretz* 11762 (Ph); East Reading, *Wilkens* 471 (Ph); Schubert, *Wilkens* 5128 (Ph); Friedensburg, *Wilkens* 5168 (Ph); Emilie, *Benner* 2926 (Ph); Bristol, *Benner* 7533 (Ph); Wakefield, *Tanger* 3065 (Ph); White Oak, *Tanger* 3043 (Ph); Spring House, *Long* 32642 (Ph); Glen Riddle, *Pennell* 2708 (Ph).

WEST VIRGINIA: Ravenswood, *Balser* 775 (GH, MBG).

VIRGINIA: Great Falls, *Hunnewell* 5895 (GH); Ashland, *Wherry & Adams* 2768 (GH); Loretto, *Fernald & Long* 14178 (Ph).

NORTH CAROLINA: French Broad River, June 4, 1918, *Ashe* (GH); Williamston, *Palmer* 39808 (AA); Middlesex, *Godfrey & White* 7027 (GH, MBG); Raleigh, *Harbison* 30 (AA); Bolton, *Palmer* 39833 (MBG, AA); Highlands, *Harbison* 9, 194, 7236, 7240 (AA), *Magee* in 1901 (GH).

SOUTH CAROLINA: Calhoun Falls, *Harbison* 1 (AA); Camden, *Palmer* 42391 (MBG).

ALABAMA: Alpine, *Harbison* 846 (AA); Auburn, *Harbison* 813 (AA).

ONTARIO: Thunder Bay, *Pease* 26323 (GH); Tobermory, *Krotkov* 7517 (GH); Agawa Bay, *Pease* 18048 (GH); Britannia, *M.-Victorin* 15585 (AA); Dalhousie Lake, *Dunbar* 10 (AA); Rockcliffe, *Macoun* 80733 (MBG, AA); Summerstown, *Jack* in 1913 (AA); Jellicoe, *Jennings* 14521 (GH); Cornwall, *Jack* in 1914 (AA); Belleville, *Macoun* in 1878 (GH); Niagara, *Macoun* 34298 (GH); Port Edward, *Macoun* 34301 (GH); Sarnia, *Dodge* 57 (GH, AA).

OHIO: Painesville, *Werner* in 1892 (GH); Columbus, *Kellerman* in 1903 (GH); Georgesville, *Werner* 54 (GH).

MICHIGAN: Whitefish Point, *Fernald & Pease* 3359 (GH); Cheboygan, *Dodge* 20 (GH); Burt Lake, *Ehlers* 1183 (GH, UI); Alpena, *Wheeler* in 1895 (GH); Walhalla, *Palmer* 40470, 40471 (AA, MBG); Port Huron, *Dodge* 71, 73 (GH); Portage Lake, *Hermann* 6497 (MBG), 6486 (GH).

INDIANA: Tolleston, *Hill* in 1894 (UI); Sheffield, *Hill* in 1876 (UI); Hammond, *A. Chase* 990 (Ph, UI); Dune Park, *Hill* in 1898, *A. Chase* 709 (UI); Mongo, *Deam* 38196, 33770, 39083, 38194, 38195 (AA); Knox, *Deam* 38251 (AA); near Rainesville, *Deam* 23107 (AA).

ILLINOIS: Sag Bridge, *Hill* in 1913 (UI); Lake Zurich, May 9, 1899, *Hill* (GH, UI); Oregon, July 9, 1905, *Hill* (UI); Lombard, *Moffatt* 1610 (UI); Chicago, *Hill* in 1890 (UI); Calumet, *A. Chase* 702, 1745 (UI); Colehour, *Hill* in 1876 (UI); Barrington, *A. Chase* 1048 (UI); Mississippi Palisades State Park, *G. N. Jones* 17143 (UI).

WISCONSIN: Trout Lake, *Fassett* 13775 (GH); Cassian, *Palmer* 27795 (MBG), 27779, 27796 (AA); Marinette, *Schuette* in 1892 (GH); Dell Prairie, *Fassett* 2823 (GH); West Salem, *Fassett, et al.* 18359 (MBG); Dane Co., *Hale* in 1861 (GH, MBG); Vermont, *Fassett* 2818 (GH); Holcombe, *Fassett & Schmidt* 15708 (GH); Devils Lake, *Fassett* 2819, 2821 (GH); Delton, *Fassett* 2820 (GH); Barneveld, *Fassett* 2822 (GH).

MINNESOTA: Brule River, *Aiton* 1004 (UI); Itasca Park, *Moyle* 216 (MBG); near Duluth, *Lakela* 2873 (MBG); Cass Lake, *Pammel* 52 (GH); Big Sandy Lake, *Rosendahl* 4983 (GH), 4980 (AA); Perham, *Rosendahl* in 1926 (GH); Fergus Falls, *Blanchard* in 1908 (AA); Center City, *Taylor* in 1892 (GH); Fort Snelling, *Mearns* in 1891 (GH); Redwing, *Sandberg* 3 (UI).

NORTH DAKOTA: Enderlin, *Bergman* 1376 (MBG).

SOUTH DAKOTA: Big Stone Lake, *Williams* in 1894 (MBG); Warrens Woods, Brookings Co., *Thornber* in 1893 (GH, MBG).

IOWA: Estherville, *Wolden* 1075, 1043, 1047, 1074, 1078 (GH); Armstrong, *Cratty* in 1902 (MBG); Iowa Lake, *Cratty* in 1900 (MBG); Oak Grove State Park, *Hayden* 10489 (MBG); Fayette, *Fink* in 1894 (GH); Ames, *Pammel* 14 (AA).

MISSOURI: Sedalia, *Palmer* 30009 (AA, MBG); Holberg, *Steyermark* 18635 (MBG).

The identity of *Amelanchier spicata,* based on *Crataegus spicata* Lam., the earliest name for the species under discussion, has long been a matter of conjecture. Lamarck says his plant was growing in the Jardin du Roi, and was supposed to be a native of Canada. Considering the close connection that existed between Canada and France in the eighteenth century, there is no reason for supposing that it might have come from a more southerly region. Several theories and speculations have been set forth in an attempt to identify Lamarck's plant, but the conclusion that has had the widest influence on the choice of nomenclature is that of Wiegand, who, in 1912, supposed it to be of hybrid origin, hence unsuitable as the type,

and therefore to be dismissed from further consideration for nomenclatural purposes. A few botanists, including Britton and Schneider, continued to use the name *A. spicata* for the common and widespread low shrub of eastern North America with racemose flowers, tomentose ovary, and usually finely toothed, few-veined leaves, but a number of others attempted to apply in various senses half a dozen different names, the majority preferring to follow Wiegand and name their specimens either *A. humilis* or *A. stolonifera*.

The nomenclatural combination *A. spicata* was first made by Karl Koch in 1869. Although there is some doubt whether his brief description is applicable to *Crataegus spicata* Lam., and it is quite clear that the names appended in synonymy belong elsewhere, the fact remains that he expressly cites Lamarck's name as the basonym, hence Koch's binomial is the one to be used for this species.

In 1932, Professor Alfred Rehder of the Arnold Arboretum of Harvard University obtained a photograph as well as a fragment of Lamarck's type in the Museum d'Histoire Naturelle, Paris. This material, now in the herbarium of the Arnold Arboretum, effectively dispels the mystery that for a century and a half has surrounded the identity of *Crataegus spicata* Lam. The photograph shows two specimens, presumably from the same plant, one a short flowering branch, and the other a twig with mature leaves. (See Pl. XI, fig. 2.) The flowers are not quite open, but their size and other characteristics are apparent from a microscopic examination of a fragment of the holotype that is also in the herbarium of Arnold Arboretum. The leaf-specimen has nine leaves, some large and roundish, others smaller and oval. The apices vary from shortly acutish to rounded and mucronulate. The margins are finely serrate almost to the rounded base. From an examination of this phototype, and of the accompanying fragment of the type, it becomes clearly evident that Lamarck's *Crataegus spicata* is the common and widespread small serviceberry of eastern North America with racemose small flowers, tomentose top of ovary, and usually rather finely toothed, few-veined leaves. Recognizing the possibility that the shrubs under consideration may comprise a somewhat polytypic species, Wiegand in 1912 attempted to distinguish two different species in this general cycle of affinity, chiefly on the basis of the shape, venation, and indentation of the leaf-blades. Specimens with more coarsely toothed and conspicuously veined blades were named *A. humilis*, while those with finer indentation and fewer, less regular veins were called *A. stolonifera*. Unfortunately, however, these characters are so extremely variable as to render them practically useless. While it is true that the coarser toothed specimens appear at first glance to be somewhat different from the finer toothed ones, all intergradations may be found. There are no supporting characters of flowers and fruits, or of geographical distribution. It is

perfectly evident from an examination of the types, as well as hundreds of other specimens, including many identified and annotated by Wiegand, that *A. humilis* and *A. stolonifera* belong to the same species, the oldest name for which is *A. spicata* (Lam.) K. Koch. Even if one (or both) of Wiegand's proposals could be maintained as a specific entity, it would have to be designated by one of the older names, *A. erecta* or *A. saxatilis* of Blanchard, which were adequately published and well supported by ample exsiccatae five years before Wiegand published *A. humilis* and *A. stolonifera*. Although, as Wiegand has pointed out, Blanchard's distributed specimens are a somewhat mixed lot, this fact does not exclude his proposed species from consideration in the matter of nomenclatural priority.

It may be of passing interest to note the historical fact that as a result of an oversight *A. humilis* was published without mention of a type specimen. Somewhat later a type was selected, but it was a specimen collected by Wiegand in 1895, not one of those previously cited with the original description. Unfortunately, this specimen, which closely resembles the type of *A. stolonifera,* does not wholly agree with the original description and the statements in the key, which call for a plant with leaves "coarsely dentate-serrate." Although of no special importance now, the subject is mentioned here as one of the factors which may have contributed to the difficulty of accurately interpreting and delimiting the species under discussion.

The true identity of a low, small-flowered shrub described in 1908 by B. L. Robinson from Blue Hill, near Milton, Massachusetts, as *A. oblongifolia* var. *micropetala* has long been in doubt. Wiegand in 1912 discussed these small-flowered plants, and concluded that they are hybrids between *A. canadensis* and *A. spicata,* and designated them by the formula *A. oblongifolia* × *stolonifera.* In 1916, after careful field studies, C. A. Weatherby (Rhodora 18:48, 49) expressed the view that the reduced petals may be due to the teratological condition known as staminody. In 1919, Ashe elevated Robinson's variety to specific rank, on the view that the plants could not be hybrids because of their general distribution and local abundance. It now seems evident from a study of a series of specimens in the Gray Herbarium and in the herbarium of the New England Botanical Club that these plants are merely small-flowered representatives of the common and widespread *A. spicata* (Lam.) K. Koch.

In 1918, W. W. Ashe described, as *A. austro-montana,* a "shrub not exceeding 4 m. in height," based on specimens from the valley of French Broad River, Transylvania County, in southwestern North Carolina. It was said to have finely serrate leaves that are pubescent beneath when young, but glabrous at maturity. The flowers are described as appearing "largely" before the leaves in 7-10-flowered, nodding, pubescent racemes,

and the fruits are said to be 10-14 mm. thick, shining and almost black when ripe, with the sepals erect or nearly so. Ashe commented that his new species was "related to *humilis* in fruit characters." However, an isotype of *A. austro-montana* in the Gray Herbarium (see Pl. XVI) which closely resembles the type of Wiegand's *A. stolonifera,* does not show some of the diagnostic characters of *A. austro-montana,* and in the shape, texture, serration, and indument of the leaves, the size, arrangement, and character of the fruit, the direction of the sepals, the shape, size, and direction of the flowering and fruiting racemes, as well as the structural characters of the flowers themselves, can be matched almost exactly by numerous specimens from nearly every part of the extensive geographical range of the common and variable *A. spicata* (Lam.) K. Koch.

10. AMELANCHIER SANGUINEA (Pursh) DC.
(Plates XVII, XVIII)

Mespilus canadensis var. γ *rotundifolia* Michaux, Fl. Bor. Am. 2:291 (1803).
Pyrus sanguinea Pursh, Fl. Am. Sept. 340 (1814); Bigelow, Fl. Bost. (ed. 2) 196
     (1824); Sprengel, Syst. Veg. 2:509 (1825).
Aronia sanguinea Nuttall, Gen. Am. Pl. 306 (1818); Eaton, Man. Bot. N. Am.
     (ed. 6) 29 (1833).
Amelanchier sanguinea DC. Prodr. 2:633 (1825); Spach, Hist. Nat. Veg. Phan.
     2:86 (1834); Hooker, Fl. Bor. Am. 1:203 (1834) ex p.; Loudon, Arb. & Frut.
     Brit. 2:875, figs. 630, 631 (1838); M. Roemer, Syn. Mon. 3:145 (1847); Britton
     & Shafer, N. Am. Tr. 439, fig. 385 (1908); Wiegand in Rhodora 14; 138, pl. 95
     (1912); Britton & Brown, Illustr. Fl. N. U.S. (ed. 2) 2:293, fig. 2332 (1913);
     Rehder in Bailey, Stand. Cyclop. Hort. 272 (1914); Hoffman in Proc. Boston
     Soc. Nat. Hist. 36:280 (1922); Wiegand & Eames, Fl. Cayuga Basin 247
     (1926); Rehder, Man. Cult. Tr. & Shr. 389 (1927); Rosendahl & Butters, Tr.
     & Shr. Minnesota 214 (1928); Peattie, Fl. Indiana Dunes 219 (1930); Rydberg,
     Fl. Prairies & Plains 437 (1932); Small, Man. Se. Fl. 637 (1933); Marie-
     Victorin, Fl. Laurent. 316, fig. 91 (1935); Nielsen in Am. Midl. Nat. 22:168,
     pl. 3 (1939); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 387 (1940).
Aronia latifolia Riddell, Suppl. Cat. Ohio Pl. 24 (1836).
Amelanchier canadensis var. γ *rotundifolia* Torrey & Gray, Fl. N. Am. 1:473 (1840),
     Fl. New York 1:225 (1843); Walpers, Rep. Bot. Syst. 2:55 (1843); Gray, Man.
     Bot. 130 (1848), (ed. 2) 126 (1856), (ed. 5) 162 (1868).
Amelanchier rotundifolia sensu M. Roem. Syn. Mon. 3:146 (1847); Britton &
     Brown, Illustr. Fl. N. U.S. 2:238 fig. 1988 (1897); Small, Fl. Se. U.S. 532
     (1903); Card in Bailey, Cyclop. Am. Hort. 57 (1904). Non (Lam.) Dum.-
     Courset 1811.
Amelanchier ovalis var. *willdenowiana* M. Roem. l.c.
Amelanchier erecta Blanchard in Torreya 7:101 (1907), ex p.
Amelanchier spicata sensu Robinson & Fernald in Gray, New Man. Bot. (ed. 7)
     460 (1908); Jones & Rand in Bull. Vermont Agr. Exp. Sta. 145:99, fig. 1,
     (1909). Non *Crataegus spicata* Lam.
Amelanchier sanguinea f. *grandiflora* Wiegand in Rhodora 14:139 (1912).
Amelanchier sanguinea var. *grandiflora* Rehder in Bailey, Stand. Cyclop. Hort.
     1:272 (1914).
Amelanchier grandiflora sensu Wiegand in Rhodora 22:149 (Oct. 29, 1920). Non
     Rehder 1920 (Sept. 6).
Amelanchier huronensis Wiegand, op. cit., 150; Nielsen in Am. Midl. Nat. 22:170,
     pl. 4 (1939).

Amelanchier amabilis Wiegand in Rhodora 23:48 (1921); House in N.Y. State Mus.
  Bull. 254:412 (1924); Wiegand & Eames, Fl. Cayuga Basin 247 (1926); Rehder,
  Man. Cult. Tr. & Shr. 389 (1927), (ed. 2) 378 (1940).

Straggling or arching slender shrubs 1-3 m. tall, the stems solitary, or
sometimes surculose and forming colonies; occasionally a small tree 4-6 m.
tall; young twigs reddish brown or grayish; winter buds conical, reddish
brown, dull, vernicose, or the scales ciliate, or sometimes pubescent on the
back; leaves commonly oval, varying to suborbicular, conduplicate in the
bud, unfolding before or with the flowers and usually about half-grown
or nearly full-grown at anthesis, densely whitish or somewhat yellowish
flocculent-tomentose beneath when young, tardily glabrous, or sometimes
the tomentum partially deciduous by flowering time, some of the leaves
sometimes retaining traces of tomentum at maturity, especially on the
veins beneath and on the petioles, but usually the fully mature leaves
nearly or quite glabrous on both surfaces; mature blades 2.5-7 cm. long,
2-5 cm. wide, the apex acutish or obtuse and more or less mucronate, the
base rounded subcordate; principal lateral veins of average leaves 11-13
pairs, conspicuous, rather close together, straight or nearly so, parallel,
the upper ones usually running straight to the margin and ending in the
teeth, the uppermost short and strongly curved and ascending; short
intermediate veins few or none; margins rather coarsely serrate-dentate
nearly or quite to the base with broad sharp spreading teeth, these usually
4-6 per cm., and about 20-30 on each side of average leaves of the fruiting
branches; petioles slender, 1-2 cm. long, glabrous, or remaining slightly
pubescent; flowers many, in ascending, spreading, or drooping 4-10-
flowered racemes 4-8 cm. long, the lower pedicels 6-18 mm. long; rachis
and pedicels pubescent; petals 5, white, or sometimes pinkish, oblanceo-
late, obtuse, those of the fully opened flowers 11-22 mm. long, 4-6 mm.
wide, more or less pilosulous on the base of the short claw; stamens about
20, the filaments glabrous; anthers 0.8-1.2 mm. long; hypanthium saucer-
shaped, 4-8 mm. in diameter, glabrous or pubescent outside, usually more
or less constricted on the very young fruit as a result of the neck of the
hypanthium being produced into a rim above the rounded summit of the
ovary; sepals triangular-lanceolate, acute, 3.5-4 mm. long, pubescent
within, usually recurved from the middle after anthesis; styles 5, glabrous,
2-3 mm. long, usually united only near the base; top of the ovary densely
tomentose; mature fruit globose or oblate-spheroidal, purplish-black,
glaucous, glabrous, 6-8 mm. in diameter, sweet, juicy, edible; pedicels 1-4
cm. long; seeds brown, smooth, obliquely lanceoloid, somewhat flattened,
about 5 mm. long and 2-3 mm. wide when well developed.

TYPE LOCALITY: "In Canada. . . . " Type in Michaux's herbarium,
Museum d'Histoire Naturelle, Paris. Phototype in the Gray Herbarium.

RANGE: Woods and thickets, rocky bluffs, shores, hillsides, and ravines, on various substrata, including limestone, sandstone, conglomerate, gneiss, schist, and quartzite, from southern Quebec to Minnesota and northern Iowa, southern Michigan, New York, and western Massachusetts; also in the mountains of western North Carolina. Flowering from the beginning of May to the early part of June; fruits ripening in July and August. Common names: round-leaved juneberry; shore shadbush.
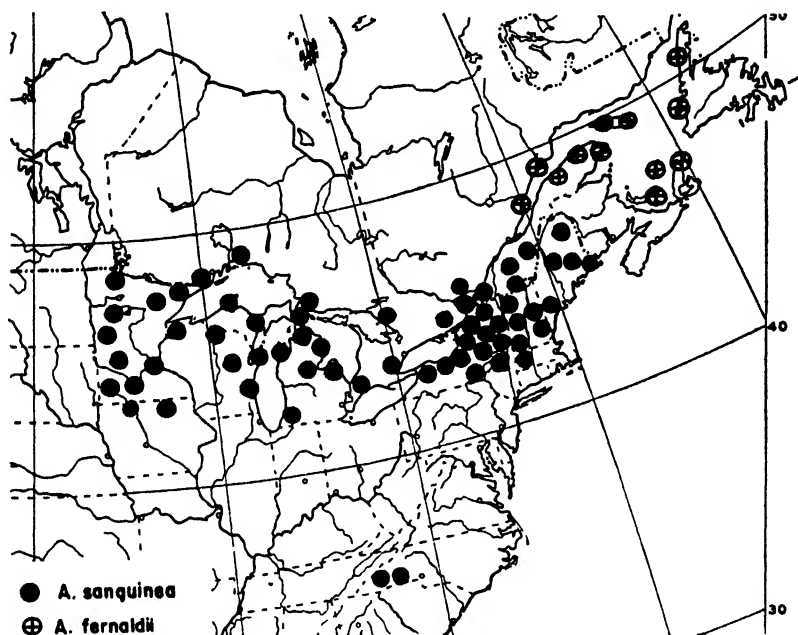
MAP 8.—Range of *Amelanchier sanguinea* and *A. fernaldii.*

QUEBEC: Isle Perrot, *Jack* 3928 (AA); Lake Massawippi, July 21, 1923, *Knowlton* (GH); Aylmer, *Rolland-Germain* 19258 (GH); Chateaugay, May 28, 1901, *Jack* (AA); Oka, *M.-Victorin* 1883 (AA), 18715 (GH); Bolton, July 25, 1926, *Knowlton* (GH); Thetford, *M.-Victorin* 11216 (AA).

MAINE: Winn, *Fernald & Long* 13780 (NE, AA); Orono, May 28, 1873, *Scribner* (NE); Veazie, June 23, 1905, *Knight* (UI); Milford, *Fernald* 13778, 13779 (GH, NE); Pembroke, *Fernald* 1880 (NE); Gilead, *Furbish* in 1897 (GH, NE); Masardis, Sept. 8, 1897, *Fernald* (NE, GH), 2311 (GH, NE); Houlton, *Fernald* in 1897 (GH, NE); Ashland, *Fernald* 2310 (GH); Fort Kent, *Woodward & Bissell* in 1914 (NE); Sangerville, *Fernald* in 1897 (NE); Dover, *Fernald* 388 (GH, NE, AA).

NEW HAMPSHIRE: Lebanon, *Fernald, Hunnewell, & Blanchard* in 1920 (NE); Haverhill, *Fernald* 15537 (GH, NE); Bath, *Pease* 19794 (NE); Durham, *Hodgdon* 2998 (NE).

VERMONT: Providence I., Lake Champlain, *Eggleston* 1178 (GH); Isle La Motte, *Cushman* 871 (NE); Swanton, May 22, 1912, *Knowlton* (NE); Mt. Willoughby, *Hodgdon* 2471 (NE); Canaan Falls, *Eggleston* 1121 (GH, UI, NE); Charlotte, May 28, 1922, *Knowlton* (NE); Burlington, *Pringle* in 1879 (AA);

Middlebury, *Brainerd* in 1901 (GH); Williamstown, June 8, 1917, *Knowlton* (NE); Wells, May 27, 1916, *Knowlton* (NE); W. Rutland, *Eggleston* 1127 (AA, NE), 1122 (GH); Hartland, May 8, 1921, *Knowlton* (NE), *Eggleston* 1971 (GH); North Hartland, *Drew, Hodgdon, & Taylor* 2472 (NE); Hartford, *Eaton & St. John* in 1920 (GH, NE); Cavendish, *Fernald* 449 (GH, NE); Bennington Co., *Steyermark* 7009 (MBG); Manchester, *Fernald, Harris, Drew, et al.* in 1932 (NE), *Cushman* 4330 (MBG); Bellows Falls, May 10, 1915, *Knowlton* (NE); Townsend, *Wheeler* in 1915 (NE); Westminster, *Blanchard* 4 (GH, AA).

MASSACHUSETTS: Sheffield, May 24, 1920, *Hoffmann* (NE); West Stockbridge, Aug. 7, 1920, *Hoffmann* (NE); Shelburne Falls, *Bean & Knowlton* 12070E (NE); Leverett, *Tower & Seymour* 3664 (NE).

NEW YORK: Canton, *Phelps* 568 (GH); Gouverneur, *Phelps* 1592 (GH); Plattsburg, *Hunnewell* 4681 (GH); Depauville, *Fernald, Wiegand, & Eames* 14302 (GH); LeRoy, *Wiegand* 13976 (GH); Romulus, *Eames* 4287, 4288 (GH); Forestport, *House* 11201 (GH); Mt. McGregor, *House* 16059 (GH); Orebed Mt., June 27, 1918, *Burnham* (GH); Lake George, *Kennedy* in 1885 (GH); Lake George Region, Aug. 10, 1916, *Burnham* (GH); Rochester, *Wiegand* 13979 (GH); Mendon, *Slavin* 205 (AA); Ledyard, *Wiegand* 6589, 6592 (GH); Glenville, *Svenson* in 1924 & 1931 (GH); Sand Lake, *Wiegand* 4281 (GH); Middleburg, *Svenson* 7849 (GH); Ithaca, *Wiegand* 2498 (GH, MBG), 2499, 2501 (GH), May 11, 1897 (GH, TYPE of *A. sanguinea* f. *grandiflora*); Caroline, June 10, 1882, *Dudley* (AA); Dryden, *Wiegand* 6582 (GH); Danby, *Wiegand* 2505 (GH); North Spencer, *Wiegand & Metcalf* 6583 (GH).

NEW JERSEY: Alpine, *Mackenzie* 5804 (Ph).

NORTH CAROLINA: Craggy Mt., near Biltmore, *Biltmore Herbarium* 5664c (GH, MBG, UI), 5664d (UI); Chimney Rock Mt., *Biltmore Herbarium* 5664e (MBG, UI, GH).

ONTARIO: Cloche Peninsula, *Fernald & Pease* 3364 (GH); Guelph, June 13, 1904, *Klugh* (GH); Port Franks, Lambton Co., May 26, 1904, *Dodge* (AA); Thessalon, *Pease & Bean* 26215 (GH); Gravenhurst, *Biltmore Herbarium* 5664 (GH, AA); Bear Island, *Krotkov* 5390 (GH); Plevna, Aug. 8, 1902, *Fowler* (GH); Nipigon, *Pease & Bean* 26502 (GH); Dalhousie Lake, *Dunbar* 12 (AA); Brockville, *Blanchard* 4 (GH); Ottawa, *Macoun* 20074 (GH).

MICHIGAN: West Bluff, Keweenaw Co., *Fernald & Pease* 3365, 3366, 3367 (GH); Copper Harbor, *Hermann* 7791 (MBG); Bête Grise, *Fernald & Pease* 3361 (GH); Gwinn, June 6, 1909, *Harrison* (GH); Mackinac I., July 4, 1912, *Hunnewell* (GH), June 2, 1900, *Schneck* (UI), *Sargent* in 1911 (AA); Cheboygan Co., *Gates* 9544 (UI), 13914 (AA); Douglas Lake, *Ehlers* 323 (GH); Sand Point, *Dodge* 74, 76 (GH, TYPE of *A. huronensis*); Sawyer, May 19, 1928, *Manning* (UI); N. Manitou I., *Wislizenus* 937.

WISCONSIN: Port Wing, *Fassett* 7313 (GH); Lake Owen, June 5, 1928, *Griscom* (GH); Rhinelander, *Palmer* 28711 (MBG); Dyckesville, *Palmer* 28747 (MBG); Ellison Bay, *Palmer* 28791 (MBG, AA); Jacksonport, *Kraus* 16 (GH); Milwaukee, May 21, 1906, *Hill* (UI); Ephraim, *Kraus* 22 (GH); Keshena, *Palmer* 27740 (MBG); Port Washington, *Palmer* 28861 (MBG); Cedarburg, *Palmer* 28905 (MBG).

MINNESOTA: Wilmar, *Palmer* 36815 (AA, MBG); Falls of Minnehaha, July 16, 1886, *L. H. Bailey* (GH); Duluth, June 28, 1915, *Stone* (Ph); Lake of the Woods, *MacMillan & Sheldon* 1747a (Minn.); Grand Portage, *Rosendahl* 6072 (Minn.); Itasca Park, *Nielsen* 1967, 2500 (Minn.); Red Wing, *Nielsen* 1349 (Minn.).

IOWA: Estherville, *Wolden* 1353 (GH); Bluffton, July 18, 1933, *Tolstead* (Minn.).

The first mention of the species under discussion was made by Michaux in 1803, who described a *Mespilus canadensis* var. *rotundifolia* as "arborescens: foliis suborbiculato-ovalibus, utrinque rotundatis . . . in Canada." The interpretation of Michaux's plant is rendered quite clear

by an examination of a photograph of the type specimen in the Michaux herbarium (Mus. Hist. Nat. Paris), which, "though not conclusive, seems more like the large-flowered, coarse-toothed species than any other; and this interpretation seems to have been that reached by other recent botanists who have studied the type. The Michaux variety was raised to specific rank and transferred to *Amelanchier* by Roemer in 1847. Unfortunately in 1814 Pursh described a *Pyrus sanguinea*. There has always been doubt as to the identity of this plant; and, so far as known, no specimen is in existence. Pursh cites as the only synonym the *M. canadensis* γ *rotundifolia* of Michaux, but he further says 'tenuissime serratis . . . A small tree . . . berries red . . .' which are not the characters of Michaux's plant. Moreover the locality is given as, 'In Canada and on the banks of the Columbia.' Since that time attempts have been made to apply Pursh's name, but in a most diverse manner (see Lindley in Bot. Register t. 1171, and Loudon, Arb. et Frut. p. 875). Evidently Pursh confused at least two plants, and evidently the only thing definite in connection with the Pursh name is the Michaux synonym, but that is definite, and the name need not be a source of confusion; therefore the writer is inclined to believe, with Dr. Britton, that Pursh's specific name should be retained for Michaux's plant. Even if Pursh's name is not used, the name *rotundifolia* can not be used as a specific name for our plant, as it is an earlier valid name[1] for the native European species." (Wiegand, in Rhodora 14:125. 1912).

The phototype (Plate XVII) of Michaux's plants depicts two fruiting specimens, almost exactly alike, mounted over three labels. On one label there is the statement "Lac Champlain," on the second, "hab. in Canada," and on the third label, "Lac Mistassin." Therefore, it is evident that Michaux's specimens came from the province of Quebec, or the northern part of what is now the state of New York, or adjacent Vermont. Clarification of the understanding of Michaux's type is contributed by a pencil tracing in the Gray Herbarium. This strengthens the conclusion of Wiegand and others that Michaux had a specimen of the taller, straggling shrub with coarsely toothed leaves and longer fruiting pedicels that we now call *A. sanguinea* (Pursh) DC.

Occasional specimens with larger flowers, and looser, often drooping racemes, have been named *A. grandiflora* Wieg., *A. huronensis* Wieg., and *A. amabilis* Wieg., or they have been treated as a variety or form of *A. sanguinea.* Since there are no evident supplementary characters of foliage or fruit, or even any differences of geographical distribution, these specimens are here considered to be well within the normal range of variation found in *A. sanguinea.*

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[1]Not valid according to the current International Rules (1935) because *Crataegus rotundifolia* Lam. is an illegitimate substitute-name for *Mespilus Amelanchier* L. The valid name for this European species is therefore *Amelanchier ovalis* Medic.

11. AMELANCHIER GASPENSIS (Wieg.) Fern. & Weatherby
(Plate XIX)

Amelanchier sanguinea sensu Lindley in Bot. Reg., pl. 1171 (1828). Non DeCandolle, 1825.

Amelanchier sanguinea var. *gaspensis* Wiegand in Rhodora 14:139 (1912).

Amelanchier florida sensu Wiegand in Rhodora 14:143, pl. 95 (1912); Rosendahl & Butters, Tr. & Shr. Minnesota 216 (1928). Non Lindley, 1833.

Amelanchier gaspensis (Wiegand) Fernald & Weatherby in Rhodora 33:235 (1931).

Low, much-branched shrubs 30-90 cm. tall, often forming dense thickets; bark grayish or brownish; winter buds conical, acute, glabrous or more or less pubescent; leaves commonly oval, varying to suborbicular, conduplicate in the bud, unfolding before the flowers and usually nearly or quite full-grown at anthesis, glabrous or quickly glabrate from the first; mature blades relatively thin, 3-6 cm. long, 1.5-4 cm. wide, the apex usually rounded or subtruncate, or somewhat acutish, the base cordate or subcordate, or sometimes rounded, quite glabrous on both surfaces, pale green beneath; primary lateral veins of average leaves 6-13 pairs, prominent, nearly equally distant, curved upward, the upper ones usually extending to the margin and ending in the teeth, the others anastomosing at their tips; margins dentate-serrate to below the middle (varying to subentire) with broad sharp ascending teeth, these usually 3-6 per cm., and about 5-20 on each side of average leaves of the fruiting branches; petioles slender, 1-2.5 (-3) cm. long, glabrous or quickly glabrate; flowers small, in ascending or erect, 5-15-flowered racemes 3-6 cm. long, the lower pedicels 1-2 cm. long; rachis and pedicels glabrous or barely pilose; petals 5, white, oblanceolate, glabrous throughout, 6-9 mm. long, 2-3.5 mm. wide; stamens 20, the filaments glabrous; anthers 0.6-0.9 mm. long; hypanthium saucer-shaped, 3-4 mm. in diameter, essentially glabrous outside, more or less constricted on the young fruit as a result of the neck of the hypanthium being produced into a rim above the rounded summit of the ovary; sepals lanceolate, acutish or acuminate, 1.5-3 mm. long, occasionally merely divaricate but usually recurved from the middle after anthesis, permanently glabrous on both sides, or with a small tuft of tomentum near the tip; styles 5, glabrous, about 2 mm. long, usually united to the middle; top of the ovary tomentose; mature fruit globose or subglobose, purplish black, glaucous, glabrous, 8-10 mm. in diameter when fully mature; lower pedicels 1-2 cm. long; seeds brown, smooth, obliquely lanceoloid, somewhat flattened, 4-5 mm. long, 2-3 mm. wide.

Type Locality: Mouth of the Bonaventure River, Bonaventure Co., Gaspé Peninsula, Quebec, Canada. Type in the Gray Herbarium; isotype in the herbarium of the Arnold Arboretum.

RANGE: On cliffs, ledges, gravelly beaches, talus, or in alluvial woods, Gaspé Peninsula, and neighboring counties of Quebec; extending northward and westward to James Bay, and the region about Lake Superior. Flowering from July to the middle of August; fruits ripe in August and September.

QUEBEC: Grand River, *Fernald* in 1904, *Richards* in 1903 (GH); Percé Mt., *Collins, Fernald, & Pease* in 1904 (GH); Mt. St. Pierre, *M.-Victorin, et al.* 33203 (AA, GH), *Fernald, Weatherby, & Stebbins* 2451 (GH); Anse Pleureuse, *M.-Victorin, et al.* 33440 (GH); Coin-du-Banc, *M.-Victorin, et al.* 17434 (GH, AA); Riviere York, *M.-Victorin, et al.* 17431 (GH, AA); Mont Louis, *M.-Victorin* 28582 (AA, GH); Grande-Coupe, *M.-Victorin, et al.* 17435 (AA, GH); Cape Rosier, *Pease* 20216 (GH); Lac Pleureuse, *Fernald, Dodge, & Smith* 25840 (GH); Mt. Ste. Anne, *Williams, Collins, & Fernald* in 1905 (GH); Rivière St. Anne des Monts, *Fernald, et al.* 25839 (GH, AA), *Collins & Fernald* in 1905 (GH); mouth of Bonaventure River, *Williams & Fernald* in 1902 (TYPE, GH; AA); Maria, *M.-Victorin, et al.* 33298 (GH); Bonaventure River, *Collins, Fernald, & Pease* in 1904 (GH); Matapedia, *M.-Victorin* 28694 (GH); Sainte-Flavie, *Rousseau* 24537, 24554 (GH); Matane, *Forbes* in 1904 (GH); Milnikek, *Rousseau* 32418 (AA); Cap Enrage, *Rousseau* 26478, 26672 (GH), 26513 (AA); Bic, *Rousseau* 26259 (GH), 26241 (AA, GH), *Collins & Fernald* in 1904 (GH), *Fernald & Pease* 25137 (GH), *Louis-Marie, et al.* 34432 (GH); Montmagny, *Rousseau* 24561 (GH); Ile à Deux Têtes, *M.-Victorin* 24538, 24558 (GH, AA); L'Islet, *Rousseau* 24550 (GH); Charlton I., James Bay, *Potter* 484 (GH); 10 miles south of East Main, *Potter* 485 (GH).

ONTARIO: 50 miles north of Jackfish, *Jennings* 14024c (GH); Twin Islands, Temagami Region, *Anderson & Anderson* 26042 (GH); Batchawana Bay, *Pease & Ogden* 25152 (GH); Awrey, Sudbury District, *Fernald & Pease* 3369 (GH).

MICHIGAN: Keweenaw Co., May and July 1889, *Farwell* (GH); Alcona Co., *Bailey* 56 (GH); Carp Lake, Ontonagon Co., *Pease & Ogden* 24884 (GH); rocky shore of L. Superior, Marquette, Aug. 2, 1889, *Hill* (UI); Isle Royale, *Cooper* 122, 124, 125 (GH).

This species is related to *A. sanguinea* (Pursh) DC., and the cordilleran *A. alnifolia* Nutt. From the former it differs in its "glabrous or quickly glabrate foliage, its leaves more commonly rounded or subtruncate at summit, its fewer nerves with anastomosing tips, its erect racemes with glabrous or barely pilose rachis and pedicels, its shorter and glabrous or promptly glabrate sepals, and its shorter petals, and occupying a clearly circumscribed area northeast of the range of *A. sanguinea*, *A. gaspensis* seems to be quite as definite a species as any in the group." (Fernald & Weatherby, l.c.). From *A. alnifolia* it may be distinguished in the fruiting condition by its glabrous somewhat longer sepals, the "thinner leaves with at most pale green lower surfaces, the cordilleran series having the coriaceous leaves glaucous beneath," and its different habit of growth, and smaller fruits, as well as the wholly distinct geographical range. Although first described as a variety of *A. sanguinea*, it appears to be probably as

closely related to *A. alnifolia.* It seems best, therefore, to follow Fernald & Weatherby in treating the Gaspé plant as a distinct species.

Amelanchier gaspensis was apparently first illustrated (as *A. sanguinea*) in 1828 by Lindley in the Botanical Register, pl. 1171, on the basis of specimens grown in the gardens of the Royal Horticultural Society, but which came originally from near the southern end of James Bay, Ontario, "whence living plants were sent . . . by William Williams, Esq., Governor of Moose Factory, in 1824." From the beautiful colored plate and the accompanying description, it is evident that the plant described and illustrated is that which is now known as *Amelanchier gaspensis.* The description contains the following statements: "A handsome hardy shrub, resembling the Snowy Mespilus [i.e., probably *A. arborea*] in general appearance, but distinguished from that, and all other species of the genus, by its *young leaves being perfectly destitute of pubescence."* (Italics mine). *A. gaspensis* is the only known species of Amelanchier that grows in the region indicated and fits the description and illustration. The only discrepancies in the plate are that the leaves are shown as being slightly more pointed than is usual in *A. gaspensis,* and the flowers have glabrous ovaries, and only 3 or 4 styles. However, these peculiarities can be safely attributed to the merely impressionistic tendencies of the artist, because all the eastern American species have 5 styles, and in the description Lindley says that the calyces are "internally woolly," and the leaves are "obtuse at each end."

During the time since *.A. gaspensis* was first recognized as a distinct entity by Wiegand in 1912, additional collections and field studies have made possible a considerable extension of the known geographical range of this species, which was at first thought to include only the Gaspé Peninsula of Quebec. The plant is now known to range westward to the region about Lake Superior. Collections of flowering specimens from Isle Royale, and others from northern Michigan, match almost exactly those from the type locality on the Gaspé Peninsula. They have the same kind of inflorescence, with the short pedicels, the glabrous and somewhat glaucous calyces, and the short petals. The obtuse leaves are fully grown and nearly or quite glabrous at flowering time, and their margins are toothed chiefly above the middle or toward the apex. In the light of subsequent discoveries it is now easily seen why Wiegand, and others, quite unable to match this material with any available specimens of the two related and somewhat similar species of the region, e.g., *A. spicata* and *A. sanguinea,* and apparently not suspecting that the plants belonged to *A. gaspensis,* arrived at the erroneous conclusion that their plants were identical with *A. florida* of the Pacific Slope of North America, whose natural geographical area is not closer than fifteen hundred miles to the westward.

12. AMELANCHIER ALNIFOLIA Nutt.
(Plate II)

Aronia alnifolia Nuttall, Gen. N. Am. Pl. 306 (1818).

Pyrus alnifolia Sprengel, Syst. Veg. 2:509 (1825).

Amelanchier alnifolia Nuttall in Journ. Acad. Nat. Sci. Philadelphia 7:22 (1834);
M. Roem. Syn. Mon. 3:147 (1847); Decaisne in Nouv. Arch. Mus. Hist. Nat.
Paris 10:135 (1874); Coulter, Man. Bot. Rocky Mt. Reg. 89 (1885); Watson in
Garden & Forest 1:185, fig. 34 (1888); Watson & Coulter, in Gray, Man. (ed.
6) 167 (1889); Sargent, Silva N. Am. 4:131, pl. 196 (1892); Britton & Brown,
Illustr. Fl. N. U.S. 2:239, fig. 1989 (1897); Koehne in Gartenflora 51:610,
fig. 126 (1902); Card in Bailey, Cyclop. Am. Hort. 57, fig. 78 (1904); Sargent,
Man. Tr. N. Am. 363, fig. 285 (1905); Rydberg, Fl. Colo. 191 (1906); Schneider,
Illustr. Handb. Laubh. 1:738, figs. 411, 412 (1906); Britton & Shafer, N. Am.
Tr. 440, fig. 387 (1908); Coulter & Nelson, New Man. Rocky Mt. Bot. 266
(1909); Apgar, Ornam. Shr. U.S. 182, fig. 278 (1910); Britton & Brown, Illustr.
Fl. N. U.S. (ed. 2) 2:293, fig. 2333 (1913); Bean, Tr. & Shr. Brit. Isles 1:186
(1914); Rehder in Bailey, Stand. Cyclop. Hort. 272, fig. 187 (1914); Arm-
strong, Field Book W. Wild Fl. 217 (1915); Rydberg, Fl. Rocky Mts. 447
(1917); Standley in Contr. U.S. Nat. Herb. 22:366 (1921); Bailey, Man. Cult.
Pl. 378 (1924); Tidestrom, in Contr. U.S. Nat. Herb. 25:283 (1925); Rehder,
Man. Cult. Tr. & Shr. 389 (1927); Kirkwood, N. Rocky Mt. Tr. & Shr. 188,
fig. 38 (1930); Rydberg, Fl. Prairies & Plains 437, fig. 290 (1932); Garrett,
Spr. Fl. Wasatch Reg. (ed. 5) 106 (1936); Nielsen in Am. Midl. Nat. 22:164,
208, pl. 1. (1939); Preston, Rocky Mt. Tr. 175 (1940); Rehder, Man. Cult.
Tr. & Shr. (ed. 2) 387 (1940).

Amelanchier ovalis sensu Hooker, Fl. Bor. Am. 1:202 (1834); Loudon, Arb. & Frut.
Brit. 2:876 (1838), ex p. Non D.C., 1825.

Amelanchier canadensis var. δ *alnifolia* Torrey & Gray, Fl. N. Am. 1:473 (1840);
Walpers, Rep. Bot. Syst. 2:55 (1843); Porter & Coulter, Syn. Fl. Col. 38 (1874).

Amelanchier montana Hort. ex Hand-list Trees Kew 1:217 (1894).

Amelanchier parvifolia Hort. ex ibid.

Amelanchier lanulosa Greene, MS.

Amelanchier cuneata Piper in Bull. Torr. Club. 27:392 (1900), Contr. U.S. Nat.
Herb. 11:346 (1906); Schneider, Illustr. Handb. Laubh. 1:739 (1906)

Amelanchier florida sensu Piper, Contr. U.S. Nat. Herb. 11:346 (1906), ex p.;
Piper & Beattie, Fl. Se. Wash. & Adj. Idaho 133 (1914); Henshaw, Wild Fl.
N. Am. Mts. 154, pl. 30 (1914); Sargent, Man. Tr. N. Am. (ed 2) 396, fig. 352
(1922); Raup in Contr. Arnold Arb. 6:174 (1934), Nat. Mus. Canada Bull.
74:142 (1935); Garrett, Spr. Fl. Wasatch Reg. (ed. 5) 106 (1936); St. John,
Fl. Se. Wash. & Adj. Idaho 194 (1937); Graham, Ann. Carnegie Mus. 26:231
(1937). Non Lindley 1833.

Amelanchier utahensis sensu Piper in Contr. U.S. Nat. Herb. 11:346 (1906). Non
Koehne 1890.

Amelanchier alnifolia var. *typica* Schneider, Illustr. Handb. Laubh. 1:739, figs. 411,
412 (1906); Nielsen in Am. Midl. Nat. 22:167 (1939).

Amelanchier alnifolia var. *pumila* Schneider, Illustr. Handb. Laubh. 1:739 (1906),
as to name only; Rehder in Bailey, Stand. Cyclop. Hort. 273 (1914).

Amelanchier macrocarpa Lunell in Am. Midl. Nat. 3:143 (1913); Rydberg, Fl.
Prairies & Plains 437 (1932).

Amelanchier leptodendron Lunell in op. cit. 5:237 (1918).

Amelanchier carrii Rydberg in Brittonia 1:89 (1931), Fl. Prairies & Plains 437
(1932).

Amelanchier humilis sensu Raup in Journ. Arnold Arboretum 17:264 (1936). Non
Wiegand 1912.

Amelanchier alnifolia f. *alba* Nielsen in Am. Midl. Nat. 22:167 (1939).

Amelanchier alnifolia var. *dakotensis* Nielsen in ibid.

Shrubs or small trees 2-4 m. tall, or in exposed situations sometimes dwarfed and prostrate; bark smooth, dark gray on the older branches, reddish brown on the branchlets; twigs of the season more or less silky-pubescent, soon becoming glabrous; winter-buds conical, villosulous, acute, dark brown, 3-6 mm. long; leaves of firm texture, oval or usually sub-orbicular or almost quadrangular, mostly flat, unfolded and more than half-grown at flowering time, tomentose beneath when young, soon becoming glabrous, usually by the time the flowers are fully expanded; upper surface dark green, smooth, quite glabrous, the lower surface pale or glaucous, glabrous throughout, or slightly pilosulous on the lower part of the midvein; blades 2-5 cm. long, 1.5-4 cm. wide, almost always obtuse, rounded, or truncate at the apex, rounded, truncate, or subcordate at the base, rarely somewhat tapering; lateral veins 8-13 pairs, conspicuous, parallel, curving and often forked and anastomosing near the margin, or running into the teeth, the intermediate veins none or inconspicuous; margins coarsely serrate or dentate to the middle, the lower half or third of the blade usually quite entire; sometimes the blade entire throughout or with 1 or 2 small teeth at apex; teeth usually coarse, rigid, ovate, acuminate, somewhat incurved, 1-3 mm. long on average leaves of the fruiting branches, 2-5 per cm., 2-20 on each side of average leaves; stipules linear, 6-18 mm. long, villous, soon deciduous; petioles 8-18 mm. long, pilose when young, soon becoming glabrous; flowers white, fragrant, conspicuous; racemes erect, 3-6 cm. long, 5-15-flowered, short and rather dense, the rachis and pedicels conspicuously lanate, the lower pedicels 5-15 mm. long; petals 5, white, oblanceolate, or oval, obtuse, 6-10 mm. long, 2-3 mm. wide, more or less ciliolate and with a small tuft of hairs on the base of the very short claw; stamens about 20, 1-2 mm. long, the filaments glabrous; anthers 0.6-0.9 mm. long; hypanthium shallowly campanulate, 3.5-4 mm. in diameter, the outside floccose at first but soon glabrous; sepals deltoid-lanceolate to lanceolate, 1.5-3 mm. long, more or less pilose within, becoming reflexed in age; styles 5, rarely 4, united below, 1.5-2.5 (-3) mm. long; summit of ovary persistently tomentose; fruit globose to obpyriform, 10-15 mm. in diameter, normally 10-loculed, and 10-seeded, purple or nearly black when ripe, glaucous, glabrous, edible, usually sweet and juicy, but the flavor rather insipid; fruiting pedicels glabrous, 5-15 mm. long; seeds asymmetrical, oval, flattened, brown, smooth, 4-5 mm. long, 3 mm. wide when fully developed.

TYPE LOCALITY: "In ravines and on the elevated margins of small streams from Fort Mandan [North Dakota] to the Northern Andes [Rocky Mountains]." Collected by Thomas Nuttall.

RANGE: Common along streams and on moist hillsides, in woods or thickets, or on open slopes in canyons and on mountainsides, from Yukon to Manitoba, southward to Nebraska, Colorado, and eastern Oregon; flowering from the middle of May to the middle of July, according to the altitude and latitude; fruit maturing in July and August. Common names: Western shadbush, saskatoon, serviceberry.

YUKON: Dawson, *Eastwood* 269 (AA), *Kusche* in 1916 (GH); Lewis River, *Gorman* 1026 (ND).

BRITISH COLUMBIA: Dawson Creek, *Raup & Abbe* 3500, 3502, 3530 (AA); Field, *Ulke* S35 (AA); Kelowna, *Murie* 1183 (MBG); Emerald Lake, *Pease* 22360 (G).

WASHINGTON: Klickitat Co., *Suksdorf* 10025, 10026 (AA, UI), 10129 (AA), 10154 (GH, AA), 10234, 10247 (AA), 11841, 11859 (UI); Pullman, *Piper* 1534 (AA), *Jack* 1213 (AA), *G. N. Jones* 1397 (GH, UI), 2057 (UI), *Beattie* 1819 (MBG); Yakima Co., *Cotton* 576, 571, 569, 365 (MBG); Spokane Co., *Suksdorf* 8597 (AA), 8609 (AA, UI), 8585 (UI), *Sandberg & Leiberg* 94 (MBG), *Palmer* 37835 (MBG), *Jack* 1453 (AA); Cle Elum, *Palmer* 37858 (AA); Easton, *G. N. Jones* 4681 (UI); Okanogan Co., *Thompson* 7073 (MBG); Kahlotus, *Rollins, Dillon, & Pickett* 868 (MBG), *Constance & McMurray* 1135 (MBG); Bishop, *Constance & Rollins* 1510 (GH).

OREGON: Strawberry Mts., *Applegate* 6219 (AA), *Ferris & Duthie* 784 (AA); Canyon City, *Brown* 78 (AA, MBG); Deschutes River, *E. Nelson* 807 (MBG); Tumalo Creek, *Whited*

MAP 9.—Range of *Amelanchier alnifolia.*

571 (MBG); Lake Co., *Ferris & Duthie* 411 (AA); Baker, *M. E. Jones* 25397 (MBG); Blue Mts., *A. Nelson & Ruth Nelson* 783 (MBG).

ALBERTA: Wood Buffalo Park, *Raup* 2645, 2647, 2648, 2650, 2652, 2653, 2654, 2656 (GH); Fort Chipewyan, *Raup* 6065 (GH); Fort McMurray, *Raup* 7078, 7089 (GH); Lake Athabaska, *Raup & Abbe* 4466, 4515, 4519 (GH); Waterways, *Raup* 2649 (GH); Jasper Park, *Jack* 2540, 2629, 2778 (AA); Lake Louise, *Hunnewell* 6169 (GH); Banff, Aug. 10, 1904, *Jack* (AA), *Brown* 23 (GH, MBG), 56 (GH); *Butters & Rosendahl* 1358 (GH), *Barber* 90 (GH); Rosedale, *Moodie* 1039 (GH); Calgary, *Moodie* 817 (GH, MBG), *Barber* 194 (GH).
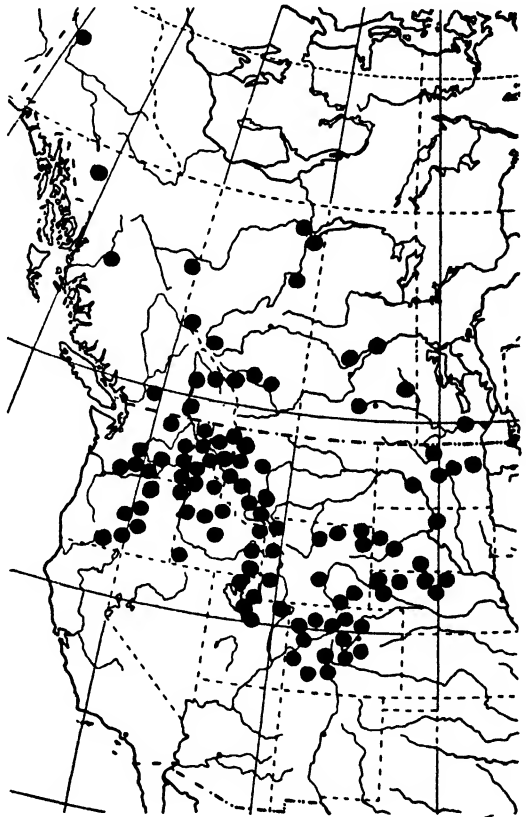
SASKATCHEWAN: Lake Athabaska, *Raup* 6670, 6588, 6931, 6084, 6933 (GH); Prince Albert, July 10, 1896, *Macoun* (GH); Moose Jaw, *Cowles* 38 (MBG, UI); Rosthern, *Munroe* in 1914 (AA); Ashcroft, *Cowles* 38a (MBG, UI); McKague, *Breitung* 523 (MBG); Saskatoon, July 14, 1913, *Sargent* (AA).

MANITOBA: Winnipeg, July 22, 1913, *Sargent* (AA); West Selkirk, *Macoun* 12627 (ND).

MONTANA: Seeley Lake, *Marsh* 507 (MBG); Bigfork, *Clemens* in 1908 (AA); Coram, *Jack* 1580 (AA); Madison River, *Scribner* in 1883 (AA); Wolf Creek, *Palmer* 36967 (AA, MBG); Great Falls, *Palmer* 36950 (MBG); Bozeman, *W. W. Jones* in 1901 (GH), *Blankinship* 135 (MBG); Gallatin Co., *Suksdorf* 52, 841 (AA); near Missoula, *MacDougal* 178 (GH), *Hitchcock* 2290 (MBG); near Bonita, *Muenscher* 11427, 11485 (MBG); Glacier Nat. Park, *Jack* 1497, 1498, 1511, 1537, 1592, 2007, 2293 (AA); St. Mary's Lake, *Hunnewell* 2445 (GH), *G. N. Jones* 5640 (UI).

IDAHO: Priest Lake, *Sargent* in 1896 (AA); near Moscow, *Jack* 1258 (AA), *G. N. Jones* in 1928 (UI); Hatwai Creek, *Sandberg, MacDougal, & Heller* 26 (GH, AA); Lewiston, *Heller* 3061 (MBG); Inkom, *Jack* 1155 (AA); Bovill, *Jack* 1359, 1374 (AA); Helmer, *Jack* 1361 (AA); Elk River, *Jack* 1336, 1379 (AA); Coeur d'Alene Mts., *Leiberg* 1203 (AA); Tamarack, *Clark* 166 (MBG); Montpelier, *Nelson & Macbride* 1052 (MBG); Salubria, *M. E. Jones* 6274 (MBG); Payette National Forest, *G. N. Jones* 5084 (GH); Salmon, *Payson & Payson* 1812 (MBG); Ashton, *Nelson* 10086 (MBG), *Cronquist & Davis* 2099 (MBG); Silver City, *Macbride* 926 (MBG); Deadwood Creek, *Nelson & Macbride* 1847 (MBG); Alturas Lake, *Cronquist* 3778 (MBG); Ketchum, *Nelson & Macbride* 1273 (MBG); Pocatello, *Jack* 1185, 1125, 1124a (AA), *Cronquist* 2298 (MBG), *Nelson & Macbride* 1405 (GH, MBG); Lava, *Nelson & Macbride* 1593 (MBG).

WYOMING: Yellowstone Nat. Park, *Jack* in 1904 (AA), *Sargent* in 1896 (AA), *Dewart* in 1889 (MBG, UI); Teton Mts., *Merrill & Wilcox* 1027a (GH); Moose, *Williams* 1106 (MBG); Upper Prairie Dog Creek, *Rollins* 550 (GH, MBG); Little Tongue River Canyon, *Williams & Williams* 3305 (GH, MBG); Cow Creek, *Nelson & Nelson* 798 (MBG); Laramie, *Jack* 1051 (AA); Dayton, *Jack* in 1900 (AA); Bighorn, *Jack* in 1900 (AA); Sundance Creek, *Nelson* 2129 (AA); Hulett, *Ownbey* 593 (MBG); Sherman, *Letterman* in 1884 (GH); Afton, *Payson & Armstrong* 3272 (MBG, GH, UI).

COLORADO: Ridgway, *Payson* 1075 (MBG); Silvercliff, *Horner* in 1898 (GH); San Juan Mts., *Wolf* 3075 (GH); Canyon City, *Nelson* 10530 (MBG); Tolland, *Palmer* 31358 (AA, MBG); Cedaredge, *Payson* 1069 (MBG); Pandora, *Baker* 750 (MBG); Estes Park, *Zobel* in 1935 (MBG); Shoshone, *Eggleston* 14967 (AA); Empire, *Engelmann* in 1874 (MBG); Sunset, *Andrews* in 1920 (AA); Boulder, *Cockerell* in 1906 (AA), *Hanson* C225 (MBG).

UTAH: Logan River, *Cronquist* 920 (MBG); Horse Creek, *Graham* 9262 (MBG); Mt. Timpanogos, *Garrett* 3686 (AA); Timpanogos Canyon, *Palmer* 38097 (MBG); Eagle Creek, *Harrison & Larsen* 7877 (MBG); Bromide Peak, *Harrison* 7473 (MBG); Thistle, *Eastwood* 7706 (AA); City Creek Canyon, *M. E. Jones* 1447 (AA); Providence Canyon, *Muenscher & Maguire* 2360 (MBG).

MANITOBA: Portage la Prairie, *Herriot* 72329 (GH).

NORTH DAKOTA: Devil's Lake, *Palmer* 36902 (AA), 36859 (MBG), *Lunell* in 1909 & 1910 (UI); Larimore, *Palmer* 36855 (AA, Ph); Butte, *Lunell* in 1907 and 1911 (AA, TYPE coll. of *A. macrocarpa*); Dunseith, *Lunell* in 1918 (TYPE coll. of *A. leptodendron*) (GH, MBG, UI); Stump Lake, *Stevens & Graves* 278 (GH); Pleasant Lake, *Lunell* in 1901 (GH); Leeds, *Lunell* in 1904 (UI).

SOUTH DAKOTA: Rosebud, *Williams*, s.n. (AA); Swan Creek, *Visher* 3308 (MBG); Timber Lake, *Shantz* 345 (UI); Deadwood, *Carr* 75 (TYPE coll. of *A. carrii*) (GH, MBG), *Palmer* 37197, 37343 (MBG, AA); Redfern, *Murdoch* 4035 (GH); Elk Canyon, *Rydberg* 680 (GH); Harney Peak, *Palmer* 37398 (MBG, AA); Piedmont, *Palmer* 37048 (MBG).

NEBRASKA: Chadron, *Pool & Folsom* in 1912 (MBG); Harrison, *Bates* 6074 (AA); Kirkwood, *Bates* 1357 (AA); Valentine, *Bates* 5928 (AA); Johnstown, *Bates* in 1898 (AA); Scottsbluff Co., Aug. 13, 1901, *H. P. Baker* (MBG).

The leaves of *Amelanchier alnifolia* are usually quite free from pubescence at maturity, and are dark green above and more or less glaucous beneath. The top of the ovary is densely tomentose, and the number of styles is uniformly five; the petals vary from 7-10 mm. in length. It is a small-flowered species, and therefore distinguished at once from the larger-flowered *A. cusickii,* which has an overlapping range, and from *A. florida,* which occupies a quite separate geographical area to the westward.

There has been a certain amount of ambiguity concerning the identity of *A. alnifolia* Nutt., caused largely, it is to be supposed, by the absence of Nuttall's original specimens, and on account of confusion with other species, particularly *A. florida* and *A. cusickii.* The original material of Nuttall was, according to his description, collected between Fort Mandan and the "Northern Andes." In his "Travels and Scientific Collections of Thomas Nuttall," Dr. F. W. Pennell (Bartonia, vol. 18, pp. 15, 16, 1936) comments as follows on this particular part of the Nuttall itinerary:

Fort Mandan, near the villages of the Mandan Indians, was not at the present town of Mandan, North Dakota, but was situated on the north side of the Missouri River in the present McLean County, and almost directly opposite the later Fort Clark. . . . All the way from the Platte River to Fort Mandan Nuttall has been telling of plants that occur on "to the Mountains" or "to the Northern Andes." These terms are evidently synonymous, and the mountains indicated lie farther up the Missouri River, but they can not be the actual Rocky Mountains for Nuttall cites no more tributary rivers above Knife River and he could not conceivably have crossed what is now Montana to the ranges known to Lewis and Clark. . . . I suppose that Nuttall must have ascended the Missouri through this rough country, until he came to where the plain that had seemed illimitable from the top of the river's bluffs at last found an end in real hills and mountains. It was no more than the northern extension of the Bad Lands and certainly could make but feeble claim to the imposing term "Northern Andes," but Nuttall evidently viewed it as an outlier of a great western mountain-system, continuous through both Americas. In reality, it did form an obvious limit to the ranges of the species he had been seeing.

It appears, therefore, that the type locality of *Amelanchier alnifolia* is probably not very far west of Fort Mandan in what is now western North Dakota.

In analyzing the probable identity of *A. alnifolia* Nutt. two facts stand out clearly. First, it is the only species known to occur in the area under consideration, and second, Nuttall's description, though brief and incomplete, gives some of its essential distinguishing characters: "Smooth; leaves roundish, the upper part toothed, pinnately nerved, under side somewhat glaucous; raceme simple, elongated; fruit black and sweet. HAB. In ravines and on the elevated margins of small streams from Fort

Mandan to the Northern Andes. OBS. A shrub 4 or 5 feet high; leaves roundish and retuse, somewhat attenuated at the base, toothed towards the summit; fruit dark purple, somewhat pruinose, very agreeable and saccharine, ripening about July and August." These statements leave no doubt as to the identity of the shrub described by Nuttall. The comment about the leaves being "attenuated at the base" is not incompatible with *A. alnifolia,* whose leaves, although usually rounded at the base, may vary on occasional specimens toward the condition mentioned by Nuttall. The suggestion has been offered that Nuttall might have had specimens of one of the eastern species, such as *A. spicata,* but this is highly improbable because that species is not known to occur so far westward.

The mature foliage of *A. alnifolia, A. florida, A. spicata,* and *A. sanguinea* often shows under certain environmental conditions a remarkable tendency toward parallel development, and therefore some herbarium specimens consisting of mature leaves only are sometimes rather difficult to separate by definite taxonomic characters. It was probably on account of this close similarity of foliage that Wiegand and others supposed the western *A. alnifolia* or *A. florida* to extend as far eastward as Minnesota and Michigan, and the eastern *A. humilis* Wieg. [*A. spicata* (Lam.) K. Koch] to occur northwestward in Canada to Mackenzie. However, flowering and fruiting specimens of these species are usually readily identified. In addition to its wholly separate westerly geographical range, *A. alnifolia* is characterized by the leaf-blades being mostly rounded or truncate at the apex, glabrous or nearly so, and almost all unfolded and more than half-grown at flowering time, coarsely toothed only above the middle, the lower half entire. There are also good taxonomic characters in the flowers.

Several names, purported to be of new species related to *A. alnifolia,* but based almost wholly on characters of the foliage, have been published from time to time. These include *A. macrocarpa* and *A. leptodendron* of Lunell, both of which appear to be based on specimens of *A. alnifolia* with unusual or abnormal foliage. In 1931 Rydberg described *A. carrii* from fruiting specimens collected in the Black Hills of South Dakota. It was said to be "related to *Amelanchier alnifolia* but differs in the short sepals and subentire leaves." A series of flowering specimens collected near the type locality in 1929 by Mr. E. J. Palmer (distributed as *A. humilis*) indicate *A. carrii* to be merely a phase of the widespread *A. alnifolia.* The name *A. carrii* is accordingly reduced to synonymy. Rydberg's statement that the leaves are "probably glabrous from the beginning" is not supported by observations made on flowering specimens.

Several specimens are known of what is supposed to be a natural bigeneric hybrid between *Amelanchier alnifolia* and a species of mountain-

ash, *Sorbus scopulina* Greene. When first discovered, this was thought to be a cross between *A. florida* and *S. sitchensis.* The Sorbus-parent was identified by the writer in 1939 as *S. scopulina.* It is now almost certain that the Amelanchier-parent is *A. alnifolia* rather than *A. florida.* If a binary name is used for this hybrid it is written × *Amelasorbus jackii* Rehder in Journ. Arnold Arb. 6:154 (1925); G. N. Jones in ibid. 20:22 (1939). *Amelanchier alnifolia* Nutt. × *Sorbus scopulina* Greene.

13. AMELANCHIER FLORIDA Lindl.
(Plate II)

Amelanchier florida Lindl., Bot. Reg. 19, pl. 1589 (1833); Spach, Hist. Nat. Veg. Phan. 2:86 (1834); M. Roem. Syn. Mon. 3:144 (1847); Decaisne in Nouv. Arch. Mus. Hist. Nat. Paris 10:136 (1874); Schneider, Illustr. Handb. Làubh. 1:739, fig. 412 (1906); Piper, Contr. U.S. Nat. Herb. 11:345 (1906); Britton & Shafer, N. Am. Trees 441, fig. 388 (1908), excl. syn.; Bean, Tr. & Shr. Brit. Isles 1:189 (1914); Piper & Beattie, Fl. Nw. Coast 200 (1915); Henry, Fl. S. Brit. Col. 183 (1915); Bean in Bot. Mag. 141, pl. 8611 (1915); Rehder, Man. Cult. Tr. & Shr. 388 (1927); Sudworth in U.S. Dept. Agric. Misc. Circular 92:134 (1927); Suksdorf in Werdenda 1:21 (1927); Benson, Contr. Dudley Herb. Stanford Univ. 2:102 (1930); G. N. Jones in Univ. Wash. Publ. Biol. 5:181 (1936); Nielsen in Madrono 4:17-21, pl. 6 (1937); G. N. Jones in Univ. Wash. Publ. Biol. 7:108 (1938); Nielsen in Am. Midl. Nat. 22:208 (1939); Applegate in Am. Midl. Nat. 22:277 (1939); Peck, Man. Higher Pl. Oregon 410 (1940); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 387 (1940); Abrams, Illustr. Fl. Pac. States 2:471, fig. 2535 (1944).

Amelanchier ovalis var. *β semiintegrifolia* Hooker, Fl. Bor. Am. 1:202 (1834); Loudon, Arb. & Frut. Brit. 2:876 (1838).

Amelanchier grandiflora Douglas ex Hooker, op. cit., pro syn. *A. botryapium.*

Amelanchier parvifolia Hort. ex Loudon, Arb. & Frut. Brit. 2:877 (1838), (ed. 2) 1854.

Amelanchier florida var. *parvifolia* Loudon, l.c.

Amelanchier alnifolia sensu Sargent in Gard. & For. 5:409, fig. 69 (1892), Silva N. Am. 4:131, pl. 196 (1892), ex p.; Dippel, Handb. Laubh. 3:389, fig. 195 (1893), excl. syn.; Howell, Fl. Nw. Am. 165 (1898); Sudworth, For. Tr. Pac. Slope 345, fig. 162 (1908). Non Nutt. 1834.

Amelanchier gormani Greene, Pittonia 4:129 (1900); Schneider, Illustr. Handb. Laubh. 1:739 (1906).

Amelanchier oxyodon Koehne in Gartenfl. 51:609, fig. 126b (1902).

Amelanchier alnifolia var. *florida* Schneider, Illustr. Handb. Laubh. 1:739, fig. 411 (1906), in Rep. Sp. Nov. Reg. Veg. 3:182 (1906); Rehder in Bailey, Stand. Cyclop. Hort. 272 (1914).

Amelanchier canadensis var. *semiintegrifolia* Farwell in Rep. Mich. Acad. Sci. 7:174 (1916).

Amelanchier vestita Suksdorf in Werdenda 1:20 (1927).

Amelanchier ephemerotricha Suksdorf, l.c.

Amelanchier ephemerotricha var. *silvicola* Suksdorf, l.c.

Amelanchier florida var. *typica* G. N. Jones, in Univ. Wash. Publ. Biol. 5:181 (1936).

Amelanchier florida f. *tomentosa* Sealy in Curtis' Bot. Mag. 160: pl. 9496, figs. a-e (1937); Rehder, Man. Cult. Tr. & Shr. (ed. 2) 387 (1940).

A slender shrub 1-5 m. tall or sometimes a small tree 10 or 12 m. tall and 15-20 cm. in diameter; branches erect; bark brownish, becoming gray, young twigs reddish brown, tomentose at first, soon glabrous; winter buds usually pubescent, purplish; leaves of thin texture at flowering time and fully expanded, oval to oblong or roundish, conduplicate in vernation, tomentulose when young, especially beneath; at maturity becoming glabrous and bright green above with the midvein impressed on the upper surface; lower surface pale green and glabrous or sparingly pubescent; blades 3-4 cm. long, 2-3 cm. wide, rounded or subtruncate at the apex, or occasionally varying to acutish, rounded or subcordate at the base; lateral veins 8-12 pairs, parallel, slightly curved upward, each vein often extending into a tooth; margins mostly entire below, coarsely toothed above the middle, or rarely below, with a few spreading deltoid teeth, the teeth 4-6 per cm., 5-20 on each margin on average leaves; blades rarely completely entire; stipules linear, villous, caducous; petioles slender, 1-2.5 cm. long, sparsely pubescent at first, soon becoming glabrous; flowers white, 2-3 cm. in diameter, fragrant; racemes erect, 4-8 cm. long, 5-15-flowered, the rachis and pedicels at first whitish pubescent but soon glabrous, the lower pedicels 8-14 mm. long; petals oblanceolate, obtuse, 12-15 mm. long (rarely shorter), 3-3.5 mm. wide, the apex obtuse, the base cuneate, more or less ciliolate on the base of the very short claw; stamens about 20, shorter than the calyx-lobes; anthers yellow, 0.5-0.7 mm. long; hypanthium campanulate, 4-5 mm. in diameter, tomentose when young, soon glabrous, slightly constricted on the young fruit; sepals deltoid-lanceolate, acute or acuminate, 2-2.5 mm. long, tomentulose at least inside at anthesis, reflexed and glabrous on the fruit; styles 5, stout, glabrous, 2-2.5 mm. long, united to the middle or above; summit of the ovary closely tomentose in anthesis, becoming nearly glabrous in fruit; fruit globose, 10-13 mm. in diameter, glabrous, glaucous, becoming purplish black at maturity, juicy, edible; lower pedicels 1-2 cm. long; seeds dark brown, glossy, about 5 mm. long and 2 mm. wide.

TYPE LOCALITY: "Northwest America," collected by David Douglas in 1825, probably along the lower Columbia River, near the present site of Vancouver, Washington.

RANGE: In open woods and on hillsides, usually near sea level, but occasionally ascending the mountains to an altitude of 5000 feet; southeastern Alaska to western Oregon and northwestern California, flowering from the beginning of March to the end of June, according to the latitude and altitude.

ALASKA: Wrangell, *Eastwood* 995 (AA, MBG); Chilkat Valley, *Walker* 1075 (GH, MBG); Old Kaasan Bay, *Cowles* 1419 (MBG, UI); along road from Hyder to Stewart, B.C., *Whited* 1197 (MBG); Yes Bay, *Gorman* 39 (ND).

BRITISH COLUMBIA: Glacier, *Brown* 283 (GH, MBG); McGillivray Creek, *Macoun* 93901 (AA); Mons, *Macoun* 93898 (GH); Skidegate, Queen Charlotte Islands, *Spreadborough* 93907 (GH); Lillooet, *Macoun* 93897 (AA), 93899 (GH); Alberni, May 25, 1917, *Carter* (GH); Jessie I., *Spreadborough* 93905 (AA); Cowichan Lake, *Spreadborough* 93906 (AA); Elk Lake, *Macoun* 93881 (AA); Nanaimo, *Macoun* 93895 (AA); Prospect Lake, *Macoun* 93883 (AA); Robertson River, *Spreadborough* 93904 (AA); Renfrew, *Rosendahl & Brand* 88 (GH, MBG); Sidney, *Sargent* in 1913 (AA), *Macoun* 93879, 93880 (GH), 93875, 93887, 93889 (AA); Victoria, *Macoun* 79796, *Eastwood* 9702, *Jack* 2865 (AA).

WASHINGTON: Chuckanut Bay, *Muenscher* 9635 (MBG); Browns Island, *Zeller* 844 (GH, MBG); Upper Valley of the Nesqually, *Allen* 214 (AA, GH, MBG); Clallam Co., *Elmer* 2512 (MBG); Seattle, *Piper* 84 (AA); Snoqualmie, May 2, 1937, *G. N. Jones* (GH); Yelm, Sept. 1, 1891, *Piper* (AA); Montesano, *Heller* 3958 (AA, GH, UI, MBG); Husum, *Suksdorf* 10033, 10201 (AA); Cape Horn, *Suksdorf* 10395, 10360, 10361 (AA); Bingen, *Suksdorf* 10154 (AA, UI, MBG), 10194, 10195, 10382, 10455 (AA), 10494, TYPE coll. of *A. ephemerotricha* var. *silvicola* (GH, UI, AA), 11841, TYPE coll. of *A. vestita,* 11859, TYPE coll. of *A. ephemerotricha* (GH), 11835, 11973 (GH, MBG, UI).

OREGON: Portland, Aug. 18, 1880, *Drake & Dickson* (GH); Waukena Falls, *Thompson* 2714 (MBG); Hood River, *Suksdorf* 2138, 2139, 2153 (AA); "Oregon, *Douglas*" (GH); Sauvies I., Apr. 1881, *J. Howell* (AA); Forest Grove, *Thompson* 616 (MBG); St. Helens, *T. Howell* 1132 (GH, MBG); Corvallis, *Steward* 230, *Epling* 5623 (MBG); Salem, *Nelson* 1071 (GH); Goshen, *Abrams* 8718 (MBG); Oakland, May 3, 1914, *Hunt* (AA); Sutherlin, *Muenscher* 15136 (MBG).

CALIFORNIA: Mendocino Co., *Bolander* 4674 (MBG).
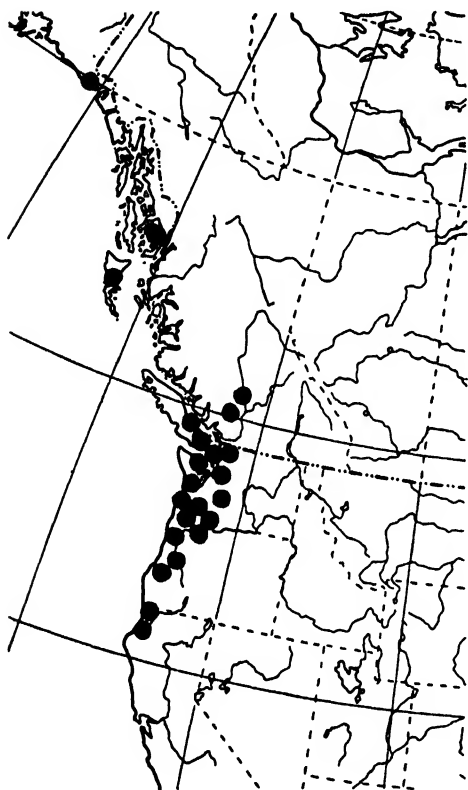
MAP 10.—Range of *Amelanchier florida.*

The identity of *A. florida* is securely established by Lindley's detailed description and excellent colored plate. It is admittedly closely related to *A. alnifolia* Nutt., and at various times the two have been treated as different species, as one species and a variety, or have been merged as a single entity. Some botanists, including Dippel, Howell, and others, while maintaining two species, have interchanged the names, a procedure that has naturally increased the confusion in an already complicated subject, and adding still further obscurity to the understanding of these species is the existence of a third, *A. cusickii* Fern., discovered in 1899, which occupies

a smaller range within that of *A. alnifolia.* Reports of *A. florida* from the region east of the Cascade Mountains, and most of the specimens so named belong really to *A. cusickii,* a large-flowered species resembling *A. florida* in superficial appearance, but immediately distinguished by the usually glabrous ovary, and longer petals and sepals. *A. alnifolia* and *A. cusickii* often grow together, but there is no evidence of hybridization between them.

Although as now recognized by critical students of Amelanchier, *A. florida* and *A. alnifolia* are distinct species with good distinguishing floral characters and separate geographical ranges (the former confined to the Pacific slope west of the Cascade Mountains, and the latter a species of the Great Plains, and the Rocky Mountain area) leaf specimens of these species are sometimes virtually indistinguishable from each other, and on that account the foliage is of limited taxonomic value. Leaves of *A. alnifolia* tend to be more nearly suborbicular and of somewhat thicker texture, and often darker green, but these are by no means constant characters, especially on specimens collected later in the season, or from drier habitats. The best distinguishing morphological character is to be found in the flowers. Flowering specimens of *A. florida* are at once distinguished from those of *A. alnifolia* by the larger flowers with longer petals. The petals of *A. alnifolia* are usually 7-10 mm. long with only occasional larger-flowered specimens. *A. florida,* on the other hand, is a relatively large-flowered plant, the petals being usually 12-15 mm. long; however, occasional smaller-flowered specimens are found on stunted plants, or plants of dry habitats, so that the distinction is not an absolute one. The habit of these two species respectively is usually somewhat different, *A. florida* being generally taller and more slender, but the growth-form of each is extremely variable according to the habitat, and can therefore scarcely serve for basic taxonomic purposes. As previously noted, the geographical ranges of the two species are almost separate, and it is only in a very few localities, such as in the Gorge of the Columbia River, that the two are ever found growing near each other.

Amelanchier gormani Greene was described from specimens collected by M. W. Gorman at Yes Bay, Alaska, in 1895, and was said to be characterized by the calyx, whose "limb is notably dilated under the insertion of the petals into a broad saucer-shaped rim; and the lanceolate segments, either erect or somewhat spreading, are longer than all the rest of the calyx, and are tomentulose within." However, this condition is by no means peculiar to specimens from Alaska, but is more or less characteristic of the partly ripened fruits of many specimens of both *A. florida* and *A. alnifolia.*

13a. AMELANCHIER FLORIDA var. HUMPTULIPENSIS
G. N. Jones

Amelanchier alnifolia var. *pumila* sensu Schneider, Illustr. Handb. Laubh. 1:739, fig. 412 (1906), as to specimen cited, non *A. pumila* Nutt. ex Torrey & Gray 1840.

Amelanchier florida var. *humptulipensis* G. N. Jones in Univ. Wash. Publ. Biol. 5:181 (1936).

Leaves and flowers smaller than those of *A. florida* var. *typica*; blades of the mature summer foliage of the fruiting branches mostly oval, acutish or obtuse at the base, acute or obtuse at the apex, 2-3 cm. long, 1-2 cm. wide, nearly entire, or shallowly serrate near the apex with small teeth; the racemes 2-4 (or sometimes only 1-2) cm. long, erect, 5-9-flowered, the pilose pedicels only 2-3 mm. long; petals 6-10 mm. long, 2 mm. wide, oblanceolate; stamens 12-15, the filaments glabrous, 1-2 mm. long; anthers 0.6-0.8 mm. long; hypanthium shallowly campanulate, sparsely pubescent outside at flowering time; sepals lanceolate, acuminate, soon recurved, 1.5-2 mm. long, glabrous within, or only sparsely pilosulous; styles 4, glabrous, unequal, 1.5 mm. long; top of the ovary tomentose, rarely nearly glabrous; fruit 5-7 mm. in diameter, 8-loculed and 8-seeded.

TYPE LOCALITY: Humptulips Prairie, Grays Harbor Co., Washington. Type: *G. N. Jones* 4565 (flower), 5819 (fruit) in the herbarium of the University of Washington, Seattle.

RANGE: Olympic Peninsula, Washington, and adjacent southern Vancouver Island, British Columbia.

BRITISH COLUMBIA: Mt. Benson, July 10, 1893, *Macoun* (GH), 208 (GH); near Victoria, May 15, 1893, *Macoun* (GH).

WASHINGTON: Humptulips, June 12, 1897, *Lamb* 1190 (AA, MBG); Humptulips River, *Murie* 1122 (MBG); Kamilche, *Benson* 1423 (MBG); Shelton, *Benson* 1420 (MBG).

This appears to be a local variety of *A. florida*, differing from the typical form of that species in its smaller size, usually more finely toothed leaves, shorter inflorescences, four styles, and its restricted geographical distribution. In 1906, C. V. Piper (Contr. U.S. Nat. Herb. 11:346) suggested that it might be a new species, but concluded that more and better specimens were needed. On account of the smaller flowers it might be treated as a near relative of *A. alnifolia* rather than of *A. florida,* but the general appearance, as well as its geographical range, suggest a closer connection with the latter, of which it might be dismissed as merely a stunted form, except for the fact that the flowers appear uniformly to possess only four styles instead of five, the almost invariable number for all other known species in this general cycle of affinity.

14. AMELANCHIER CUSICKII Fern.
(Plates III, XX)

Amelanchier cusickii Fernald in Erythea 7:121 (1899); Piper in Contr. U.S. Nat. Herb. 11:346 (1906); Schneider, Illustr. Handb. Laubh. 1:735, figs. 409, 410 (1906); Piper & Beattie, Fl. Se. Wash. & Adj. Idaho 133 (1914); Henry, Fl. So. British Columbia 183 (1915); Rydberg, Fl. Rocky Mts. 446 (1917); Kirkwood, N. Rocky Mt. Tr. & Shr. 190 (1930); St. John, Fl. Se. Wash. & Adj. Idaho 194 (1937); Peck, Man. Higher Pl. Oregon 410 (1940); Abrams, Illustr. Fl. Pac. States 2:471, fig. 2533 (1944).

Shrubs 1-3 m. tall, with numerous slender, virgate, flexible branches; bark on the young branches reddish, later becoming gray; twigs of the season reddish brown, often somewhat glossy, quite glabrous; winter buds reddish, nearly or quite glabrous, the inner scales more or less ciliate; leaves commonly oval, thin, glabrous from the first, even when young, becoming coriaceous in age, conduplicate in the bud, usually unfolded at anthesis; mature blades 2.5-5 cm. long, 2-3 cm. wide, the apex acutish and apiculate on some leaves, obtuse and rounded on others, the base rounded or subcordate, perfectly glabrous on both surfaces; lateral veins 7-10 pairs, curving upward and anastomosing near the margin; margins sharply serrate mostly above the middle, the upper teeth more prominent; teeth 3-6 per cm., 3-15 on each side on average leaves of the fruiting branches; stipules linear, deciduous, villous, about 1 cm. long; petioles slender, soon glabrous, 6-22 mm. long; flowers large, in 3-8-flowered racemes 2-5 cm. long, the lower pedicels 8-12 mm. long, glabrous; petals 5, white, glabrous, obovate or oblanceolate, obtuse, 16-25 mm. long, usually 5-7 mm. wide above the middle, the apex obtuse or acutish; stamens about 20, the filaments glabrous, 3-4 mm. long; anthers ellipsoid, 1-1.5 mm. long; hypanthium shallowly campanulate or saucer-shaped, glabrous within and outside, 4-5 mm. in diameter; sepals lanceolate, acuminate, or acute, 3.5-5 mm. long, pilose within at flowering time, usually recurved from the middle during or after anthesis, the margins very narrowly hyaline; styles 5 or 4, glabrous, 3-4 mm. long, united below the middle, or nearly free to the base; summit of the ovary glabrous or with a ring of tomentum around the base of the styles; mature fruit glabrous, globose, juicy and edible, reddish at first, becoming bluish black, about 1 cm. in diameter; fruiting pedicels 5-20 mm. long; seeds brown, smooth, asymmetrical, 4-5 mm. long.

Type Locality: "On stony hillsides, Union County, Oregon." Type (*Cusick* 1858) in the Gray Herbarium of Harvard University; isotype in the herbarium of the Missouri Botanical Garden.

RANGE: Common on basaltic ledges along rivers, British Columbia, southward to eastern Washington, eastern Oregon, Idaho, western Montana, and northern Utah; flowering in March and April; fruit ripening in June.

BRITISH COLUMBIA: Kamloops, June 30, 1887, *Fowler* (MBG).

WASHINGTON: Fort Colville, *Lyall* in 1861 (GH); Camden, *Spiegelberg* 341 (GH); Kettle Falls, *Boner & Weldert* 172 (GH, MBG); Spokane, Sept. 1, 1899, *Piper* (GH), 2694 (AA), *Suksdorf* 8575 (AA, GH, MBG, UI), *Milburge* 258 (AA); Grand Coulee, *Rollins* 840 (MBG); Blewett Pass, *Benson* 1283 (MBG); Wenatchee R., Chelan Co., *G. N. Jones* 6573 (UI); Entiat, *Thompson* 6002 (GH, MBG); Priest Rapids, *G. N. Jones* 6349 (GH); Yakima, *G. N. Jones* 1387 (UI); near Ellensburg, *Eyerdam* 1377 (MBG), *Thompson* 11386 (GH, MBG); six miles s.w. of Pullman, Aug. 4, 1899, *Piper* (GH), *Elmer* 135 (MBG); Wawawai, *Piper* 3812 (GH), *G. N. Jones* 1398 (UI); Almota, *Constance, et al.* 1037 (GH, MBG); Bishop, *Constance & Rollins* 1512 (GH); Hooper, *Constance & Rollins* 1499

MAP 11.—Range of *Amelanchier cusickii.*

(MBG); Waitsburg, *Horner* B183 (GH); Palouse Falls, *G. N. Jones* 2832 (Ph).

OREGON: The Dalles, *Lunell* 50 (GH), Apr. 19, 1903, *Lunell* (UI); Canyon Creek, Grant Co., *Henderson* 5147 (GH, MBG); eastern Oregon, *Cusick* 1858 (TYPE, GH, isotype, MBG); Wallowa Mts., *G. N. Jones* 7088, 7101, 7134, 7147 (UI); Jim Creek, Wallowa Co., *Constance* 999 (MBG); Crooked River, *Whited* 363 (GH, MBG).

IDAHO: Spalding, *Meyer* 1428 (MBG); Snake River Canyon, Idaho Co., *Constance, Clements, & Machlis* 1008, *Packard* 371, *Meyer* 854 (MBG); Dry Buck, Boise Co., *Macbride* 852 (GH, MBG); Kootenai Co., July 1890, *Leiberg* (GH).

MONTANA: Near Butte, *Moore* in 1893 (MBG); Mt. Sentinel, *Kirkwood* 28, 29, 30 (AA), *Barkley & Osburnson* 2313 (AA, MBG, UI); near Missoula, *Kirkwood* 1182 (GH, MBG), *Hughes* 1185 (GH, MBG), *E. C. Faust* in 1915 (UI); near Bonner, *Geil* 4 (MBG, UI).

UTAH: Cache Co., Logan Canyon, *Maguire* 3501 (GH); Blacksmith Canyon, *Maguire* 3507 (GH); Sardine Canyon, *Maguire* 2363 (GH).
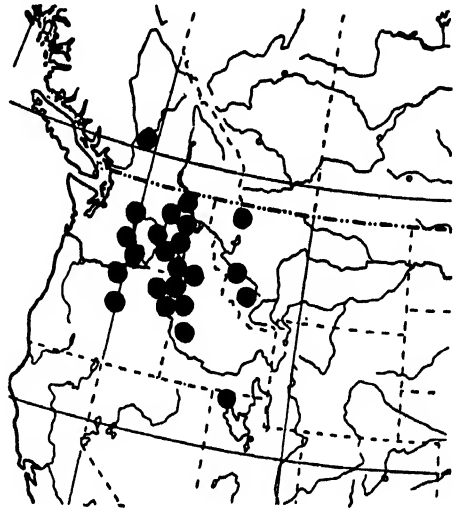
This distinctive species was named in compliment to the pioneer Oregon botanist, William Conklin Cusick (1842-1922). It is the largest-flowered species of Amelanchier, and thus in the flowering stage is at once distinguishable from all others. It blooms from ten to fifteen days earlier than *A. alnifolia.* Fruiting specimens are frequently less easily recognized, but the long sepals will usually serve to separate it from *A. alnifolia,* the common species occurring within its range.

15. AMELANCHIER BASALTICOLA Piper
(Plate III)

Amelanchier alnifolia sensu Holzinger in Contr. U.S. Nat. Herb. 3:224 (1895).
Non Nuttall, 1834.
Amelanchier basalticola Piper, Fl. Palouse Reg. 100 (1901); Piper in Contr. U.S.
Nat. Herb. 11:346 (1906); Piper & Beattie, Fl. Se. Wash. Adj. Ida. 133 (1914);
Rydberg, Fl. Rocky Mts. 446 (1917); St. John, Fl. Se. Wash. & Adj. Ida. 194 (1937).

Shrubs 1-3 m. tall; bark gray; twigs of the season glabrous, brown, smooth; winter buds small, glabrous; leaves conduplicate in vernation, appearing before the flowers, flat and unfolded at flowering time, pale green, glabrous, and glaucous from the first, firm in texture; blades suborbicular, 1.5-3 cm. long, 1.5-2 cm. wide, rounded or truncate at apex and base, the apex sometimes acute and mucronate; lateral veins 10-13 pairs, curved upward, anastomosing near the margin; margins serrate above the middle or less commonly from near the base, the teeth small, sharp, somewhat curved, 4-6 per cm., mostly 5-15 on each side on average leaves of the flowering branches; some of the blades sometimes nearly or quite entire; stipules linear-subulate, small, glabrous, fugacious; petioles slender, glabrous, 7-18 mm. long, usually shorter than the blade; flowers appearing after the leaves have unfolded, about 3 cm. in diameter; racemes terminal, 2-4 cm. long, 4-8-flowered; pedicels nearly or quite glabrous, and somewhat glaucous, 4-8 mm. long; petals 5, white, glabrous, oblanceolate, 12-16 mm. long, 3-4 mm. wide above the middle, the apex acute, obtuse, entire or erose; stamens about 20, the filaments glabrous, 2-3 mm. long; anthers 0.8 mm. long; hypanthium campanulate, glabrous and somewhat glaucous, 3 mm. in diameter, sepals linear-lanceolate, attenuate-acuminate, 3.5-4 mm. long, pilosulous within, becoming reflexed after anthesis, somewhat glaucous, slightly longer than the tube; styles 5, free to below the middle or almost to the base, 2-2.5 mm. long, summit of the ovary glabrous or nearly so; mature fruit globose, dark purple, juicy, glabrous, 9-12 mm. in diameter; fruiting pedicels glabrous, about 1 cm. long; well developed seeds chestnut brown, smooth, glabrous, 5-6 mm. long, 3-3.5 mm. wide, asymmetrical, flattened-ellipsoid, bluntly pointed at each end.

TYPE LOCALITY: Bluffs of Snake River, Whitman County, Washington, opposite Clarkston.

RANGE: Southeastern Washington, adjacent Idaho, and Oregon. Flowering in April and May; fruit ripe in June and July.

WASHINGTON: Bluffs above Wawawai, *Piper* 3823 (MBG, AA, GH).

IDAHO: Near Lewiston, Apr. 15, 1896, *Heller* (UI), 2988 (MBG, Ph); Upper Ferry, Clearwater River, near Lewiston, *Sandberg, MacDougal, & Heller* 53 (MBG, AA, GH, UI); Nez Perces Co., May 1892, *Sandberg* (UI, MBG); near Riggins, *G. N. Jones* 972 (UI).

OREGON: Mitchell, *Ferris & Duthie* 656 (AA); Wallowa River, *G. N. Jones* 7137 (UI); Deep Creek, Snake R. Canyon, Wallowa Co., *Constance, Rollins, & Dillon* 1568 (GH); Snake R. Canyon above Rogersburg, *Meyer* 226 (MBG).

Amelanchier basalticola Piper is a species of local distribution inhabiting the basaltic cliffs and ledges of the river canyons of southeastern Washington, and adjacent Idaho and Oregon. It is very conspicuous in the spring when in bloom, marking the ledges on which it grows. It belongs to the *alnifolia-florida-cusickii* cycle of affinity, being probably most closely related to *A. cusickii,* from which it differs in its shorter and narrower petals, somewhat longer sepals, and the smaller, roundish, pale green leaves. It is distinguished from *A. alnifolia* by the longer petals, longer and narrower sepals, as well as the usually smaller leaves.

16. AMELANCHIER PUMILA Nutt.
(Plates III and IX)

Amelanchier canadensis var. ε *pumila* Nuttall ex Torrey & Gray, Fl. N. Am. 1:474 (1840); Walpers, Rep. Bot. Syst. 2:55 (1843); Dietrich, Syn. 3:158 (1843).
Amelanchier pumila Nuttall ex Torrey & Gray apud M. Roemer, Syn. Mon. 3:145 (1847); Rydberg, Fl. Rocky Mts. 446 (1917); Tidestrom in Contr. U.S. Nat. Herb. 25:283 (1925); Graham in Ann. Carnegie Mus. 26:232 (1937).
Amelanchier glabra Greene, Fl. Franciscana 52 (1891); Schneider, Illustr. Handb. Laubh. 1:735 (1906); Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909); Smiley in Univ. Calif. Publ. Bot. 9:230 (1921); Tidestrom in Contr. U.S. Nat. Herb. 25:283 (1925); Abrams, Illustr. Fl. Pac. States 2:471, fig. 2532 (1944), excl. syn.
Amelanchier polycarpa Greene, Pittonia 4:127 (1900); Schneider, Illustr. Handb. Laubh. 1:735, fig. 409 (1906); Rydberg, Fl. Colorado 191 (1906); Wooton & Standley in Contr. U.S. Nat. Herb. 19:323 (1915); Rydberg, Fl. Rocky Mts. 446 (1917); Tidestrom in Contr. U.S. Nat. Herb. 25:283 (1925); Tidestrom & Kittell, Fl. Ariz. & New Mexico 251 (1941); Kearney & Peebles in U.S. Dept. Agric. Misc. Publ. 423:393 (1942).
Amelanchier alnifolia pumila A. Nelson in Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909).

Shrubs 1-3 m. tall, the whole plant perfectly glabrous; bark reddish brown, becoming gray; twigs and winter buds glabrous; leaves oval, perfectly glabrous throughout from the beginning, thickish, somewhat coriaceous at maturity, pale and somewhat glaucescent, at least on the lower surface, deeper green above; conduplicate in vernation, unfolding before or with the flowers and nearly full grown at anthesis; mature blades suborbicular to oval, 1-5 cm. long, 1-2 cm. wide, the apex obtuse or truncate, often somewhat mucronate, the base rounded, subcordate, or truncate, rarely somewhat cuneate; lateral veins 7-9 pairs, curving upward and often extending into the teeth, or anastomosing near the margin; margins coarsely serrate to the middle, the lower third of the blade entire, the teeth 1-2 mm. long, 3-5 per cm., 6-10 on each side of average blades of the flowering and fruiting branches; some small-leaved specimens with the blades nearly entire, or with only a few small teeth near the apex; stipules linear, glabrous, fugacious; petioles rather slender, mostly shorter than the blade, glabrous; flowers in erect or ascending

4-8-flowered racemes 2-4 cm. long, the lower pedicels about 6-12 mm. long; hypanthium and pedicels completely glabrous, more or less glaucous; petals 5, white, glabrous, oval, 8-12 mm. long, 3-4 mm. wide, obtuse at the apex or sometimes acute, widest at or above the middle; stamens 12-15, the filaments glabrous, 1-2 mm. long; anthers 0.8 mm. long; hypanthium campanulate, 3-4 mm. in diameter, completely glabrous, somewhat constricted on the young fruit; sepals triangular-lanceolate to linear-lanceolate, acuminate, completely glabrous on both sides, 3 mm. long (rarely longer), soon recurved; styles 5 (or 4), united at the base, glabrous, 1-2 mm. long; top of the ovary completely glabrous; mature fruits depressed-globose, dark purple, glaucous, juicy, 8-9 mm. in diameter; pedicels 6-12 mm. long; seeds brown, asymmetrical, 4-5 mm. long.

TYPE LOCALITY: "Near the sources of the Platte in the Rocky Mountains." Collected by Thomas Nuttall. Type in the herbarium of the Academy of Natural Sciences of Philadelphia.

RANGE: On mountain sides and plains, altitude 7,000-10,000 feet, southwestern Montana and Idaho, to southern Oregon, Wyoming, Utah, Colorado, and northeastern California, apparently not common, or at least only locally abundant.

MONTANA: Spanish Basin, Madison Range, *Flodman* 545 (MBG); Helena, May 1893, *Starz* (MBG).

IDAHO: Alturas Lake, *Cronquist* 2596 (MBG); Twin Falls, *Nelson & Macbride* 1368 (MBG, GH); Corral, *Macbride & Payson* 2880 (GH, MBG).

OREGON: Cougar Peak, Lake Co., *Eggleston* 7066 (GH).

WYOMING: Jackson Hole, June 9, 1934, *Nelson & Nelson* (MBG); Medicine Bow Mts., *Rollins* 889 (MBG); Laramie Hills, *Nelson* 1931 (GH, MBG); near Leckie, *Merrill & Wilcox* 548 (GH), *Sherman,* July 29, 1884, *Letterman* (MBG).

COLORADO: "R. Mts." [Rocky Mountains], *Nuttall* (TYPE in herb. Acad. Nat. Sci. Phila.); Gunnison Canyon, *Payson* 1051 (MBG); Cerro Summit, *Baker* 49 (MBG); Piedra, July 10, 1899,. *Baker* 379 (AA, GH, MBG; ND, TYPE of *A. polycarpa*); Eldora to Arapahoe Peak, *Daniels* 909 (MBG); without definite locality, *Vasey* in 1868 (GH).

UTAH: Logan Canyon, *Mulford* 192 (MBG, UI); Milford, *Hill* 169 (UI); near Moon Lake, *Harrison & Larsen* 7685 (MBG); Oak City, *Harris* C28699 (MBG).

MAP 12.—Range of *Amelanchier pumila.*

CALIFORNIA: Deer Park, Lake Tahoe region, *Eastwood* 372 (GH, AA); Donner Lake, *J. Torrey* 126 (GH, Paratype of *A. glabra*), *Heller* 7176 (GH, AA, MBG).
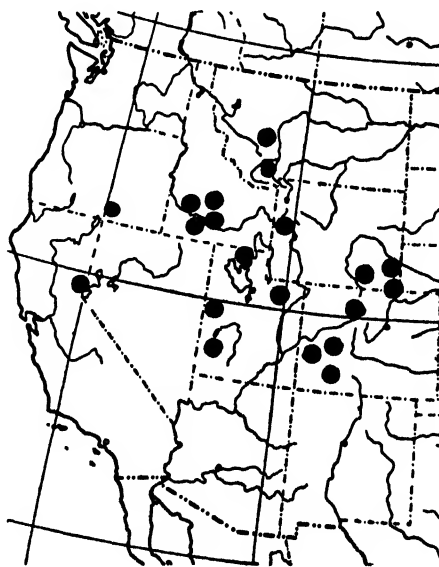
Amelanchier pumila Nutt., included in their Flora of North America by Torrey & Gray in 1840, was based on specimens collected by Nuttall "Near the sources of the Platte in the Rocky Mountains." It can usually be distinguished from all other species by the fact that the whole plant is completely glabrous, even on the youngest parts. It is evidently closely related to *A. cusickii* and *A. basalticola,* from which it differs principally in its glabrous condition, and in the smaller flowers with shorter petals, styles, and anthers.

17. AMELANCHIER PALLIDA Greene

(Plates III and XXI)

Amelanchier alnifolia sensu Brewer & Watson, Bot. Calif. 1:190 (1880); Greene, Man. Bot. Bay Reg. 110 (1894); Jepson, Fl. W. Middle Calif. 288 (1901), (ed. 2) 213 (1911); H. M. & C. C. Hall, Yosemite Fl. 125 (1912); Jepson, Man. Fl. Pl. Calif. 509, fig. 508 (1925), Fl. Pl. Calif. 2:234 (1936); McMinn, Illustr. Man. Calif. Shr. 216, fig. 239 (1939). Non Nuttall, 1834.

Amelanchier pallida Greene, Fl. Franciscana 53 (1891); Coville in Contr. U.S. Nat. Herb. 4:97 (1893); Howell, Fl. Nw. Am. 165 (1898); Schneider, Illustr. Handb. Laubh. 1:742, figs. 416, 417 (1906); Davidson & Moxley, Fl. S. Calif. 206 (1923); Tidestrom in Contr. U.S. Nat. Herb. 25:284 (1925); Benson in Contr. Dudley Herb. Stanford Univ. 2:103 (1930); Graham in Ann. Carnegie Mus. 26:232 (1937); Peck, Man. Higher Pl. Oregon 410 (1940); Abrams, Illustr. Fl. Pac. States 2:472, fig. 2538 (1944).

Amelanchier subintegra Greene in Pittonia 5:109 (1903); Schneider, Illustr. Handb. Laubh. 1:742, figs. 416, 417 (1906).

Ameianchier gracilis Heller in Muhlenbergia 2:59 (1905); Schneider, Illustr. Handb. Laubh. 1:735 (1906); Benson in Contr. Dudley Herb. Stanford Univ. 2:103 (1930); Abrams, Illustr. Fl. Pac. States 2:471, fig. 2536 (1944).

Amelanchier siskiyouensis Schneider, Illustr. Handb. Laubh. 1:735, figs. 409, 410 (1906), in Fedde, Rep. Sp. Nov. 3:181 (1906); Smiley in Univ. Calif. Publ. Bot. 9:230 (1921).

Amelanchier recurvata Abrams in Bull. Torr. Club 37:151, fig. 1 (1910); Davidson & Moxley, Fl. S. Calif. 206 (1923).

Amelanchier alnifolia var. *pallida* Jepson, Man. Fl. Pl. Calif. 509 (1925), Fl. Calif. 2:234 (1936); Munz, Man. S. Calif. Bot. 229 (1935).

Amelanchier alnifolia var. *cuyamacensis* Munz in Bull. S. Calif. Acad. Sci. 31:65 (1932), Man. S. Calif. Bot. 229 (1935).

Amelanchier alnifolia var. *siskiyouensis* Jepson, Fl. Calif. 2:234 (1936).

Amelanchier alnifolia var. *subintegra* Jepson, ibid.

Amelanchier florida sensu Wynd in Am. Midl. Nat. 17:921 (1936); Applegate in ibid. 20:277 (1939). Non Lindley 1833.

Shrubs 1-3 (-8) m. tall, with erect or ascending or divaricate branches, these often numerous and rigid, especially in dry habitats, or rarely spreading or more or less drooping; bark of the twigs and branches usually reddish brown, or gray, glabrous; winter buds pubescent; leaves oval or elliptical to suborbicular or broadly obovate, rather thick or coriaceous, indistinctly reticulate, pale dull green on both surfaces, the lower surface usually paler than the upper, or sometimes the upper surface dark green, finely tomentulose or puberulent on both surfaces,

occasionally varying to nearly or quite glabrous; blades at maturity 2-4 cm. ·long, 1.5-2.5 cm. wide, the apex usually narrow and acutish or rounded and retuse, rarely truncate, often apiculate or cuspidate, the base rounded; lateral veins 7-9 pairs, obscure; margins variable, entire or with a few small teeth toward the apex, or sometimes toothed to below the middle, both conditions often found on the same specimen; stipules linear, villous, 1-1.5 cm. long, fugacious; petioles 6-12 mm. long, usually more or less pubescent; flowers in short and somewhat corymbose racemes 2-4 cm. long and 4-6-flowered, on short lateral leafy spurs of the season; pedicels rather stout, 3-5 mm. long, pubescent at anthesis; petals 5, white, oval or obovate, 8-11 mm. long, 3-4.5 mm. wide, sparsely pilose at the base within; stamens about 15, the filaments glabrous, 2 mm. long; anthers 0.8-1 mm. long; hypanthium shallowly campanulate, 3-4 mm. in diameter, more or less tomentose on the outside at anthesis, or nearly glabrous, more or less constricted on the very young fruit; sepals lanceolate, acuminate 2-3 mm. long, villosulous on both sides, usually recurved from the middle after anthesis; styles 4 or 3 (rarely 5), glabrous, about 2 mm. long, free nearly to the base; summit of the ovary usually tomentose, sometimes only sparsely pilose or nearly glabrous; mature fruit subglobose, purplish black, juicy when mature, 4-6 mm. in diameter, the upper part of the hypanthium constricted on the young fruit; fruiting pedicels 3-9 mm. long.

TYPE LOCALITY: Near Yreka, Siskiyou County, California, collected May 12, 1876, by E. L. Greene, no. 779.

RANGE: On dry gravelly ridges and slopes, on moraines, in rocky woods and thickets, or along streams, from sea level to 8500 feet altitude, southern Oregon to southern California, chiefly in the Sierra Nevada and Coast Ranges; also in northwestern Nevada. Flowering from the middle of April to the end of June, according to the altitude; fruits ripening in July and August. Common name: California serviceberry.

OREGON: Reston, *Peck* 3530 (GH) ; near Klamath Falls, *Wiggins* 4631 (GH) ; Crater Lake National Park, *Stanford* 1758 (MBG), *G. N. Jones* 7690 (UI) ; opposite Ashland, *T. Howell* in 1889 (MBG) ; near Ashland, *Peck* 9242 (GH, MBG) ; near Waldo, Aug. 24, 1904, *Rehder & Jack* (AA), *Henderson* 5824 (MBG) ; Wilderville, Aug. 24, 1904, *Jack* (AA) ; between Rogue R. and Union Creek, *Heller* 12962 (GH, Ph, UI) ; Obrien, *G. N. Jones* 7755 (UI) ; Agness, *Nelson* 1475 (GH) ; Harbor, *Peck* 8731 (MBG, GH) ; Port Orford, *Peck* 8512 (GH, MBG).

CALIFORNIA: Shelley Creek, *Eastwood* 12076 (AA) ; French Hill, *Eastwood* 72 (AA) ; near Mt. Eddy, *Heller* 13396 (MBG) ; Siskiyou Co., *Pringle* in 1882 (GH, AA, MBG) ; near Shasta Springs, *Heller* 7970 (GH, AA, MBG, TYPE coll. of *A. gracilis*) ; Mt. Shasta, *Brown* 557 (MBG) ; Cantara, *Eastwood* 11931 (AA) ; McCloud, *Eastwood* 1081 (GH, AA) ; Weed, *Smith* 284 (GH, AA) ; Yreka, *Heller* 8003 (GH, AA, MBG), *Greene* 779 (GH, MBG, TYPE coll.) ; near Alturas, *C. L. Hitchcock* 6701 (MBG) ; Parker Creek, *Ferris & Duthie* 77 (AA) ; Hoopa Indian Reservation, *Chandler* 1282 (AA, GH, MBG) ; Little Van Duzen R., *Eastwood & Howell* 4800 ·(AA) ; Goose Valley, *Eastwood* 785 (AA, GH) ; Bennett Spring, Tehama Co., *Heller* 13004 (GH, AA, MBG, UI) ; Fredonyer Pass, *Heller* 15144

(UI); Plumas Co., *Eggleston* 6235, 7596 (GH); Mt. Sanhedrin, *Heller* 5961 (GH, MBG), *Bacigalupi* 1549 (GH, AA); Lakeport, *Baker* 2964 (GH, AA, MBG, TYPE coll. of *A. subintegra*); near Stirling, *Heller* 13156 (GH, MBG, UI); Chico Meadows, *Heller* 11963 (GH, AA, UI); near Donner Lake, *Heller* 7038 (GH, AA, MBG); Truckee, *Sonne* 88 (MBG); Emigrant Gap, *Heller* 12729 (GH, UI); Fallen Leaf Lake, *Abrams* 4809, 4817 (GH), *Smiley* 214, 215 (GH); Sebastopol, *Pammel & Davy* 77 (MBG); Heller* 5794 (GH, MBG); Cazadero, *Heller* 6617 (AA, GH, MBG); Napa, *Smyth* in 1899 (GH); Silver Lake, *Hansen* 230 (GH, MBG, TYPE coll. of *A. siskiyouensis*); San Mateo Co., *Abrams* 5577 (AA); Pescadero, *Elmer* 4659 (MBG); Santa Clara Co., *Heller* 7419 (GH, AA, MBG), *Heller* 8531 (GH, UI); Yosemite Nat. Park, *Smiley* 899 (GH), *Abrams* 4577 (GH), 4675 (AA, GH); Mt. Bullion, *Congdon* 31 (GH); Ranch Jolon, *Brewer* 576 (GH, MBG); General Grant Park, *Culbertson* 4647 (GH, MBG); Tehachapi Mts., *Abrams & McGregor* 490 (GH, AA); Topatopa Mts., *Abrams & McGregor* 107 (AA, GH, TYPE coll. of *A. recurvata*); Cuyamaca Lake, *Munz* 8099 (GH, TYPE coll. of *A. alnifolia* var. *cuyamacensis*), *Munz & Johnston* 12638 (AA, MBG), *Spencer* 865 (GH), *Abrams* 3912 (GH, MBG).

NEVADA: Verdi, June 1, 1893, *Sonne* (MBG), *Heller* 10875 (AA, GH, UI, MBG); Kings Canyon, Ormsby Co., *Baker* 952 (GH, AA, MBG), 1219 (GH, AA).
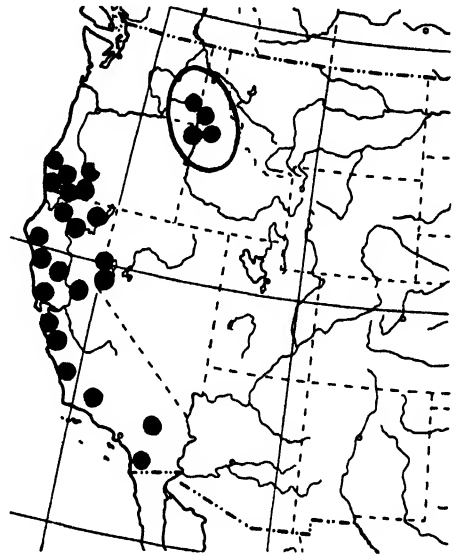
MAP 13.—Range of *Amelanchier pallida.*
In oval, *Amelanchier basalticola.*

It has been customary to refer nearly all the Californian Amelanchiers to *A. alnifolia* Nutt., but that species does not occur in California, or indeed on the Pacific slope. The common and characteristic species of California and southern Oregon is *A. pallida* Greene. It differs from *A. alnifolia* in its usually smaller, narrower leaves, which are mostly finely and inconspicuously permanently pubescent or puberulent, at least beneath, the indument scarcely noticeable to the naked eye. In fact, the original description does not mention this character. Only rarely are the leaves quite glabrous on both surfaces at maturity. The blades are variable in shape, texture, and degree of serration, varying apparently with the habitat and the age of the branch, those on vigorous young shoots often showing a tendency toward being suborbicular and coarsely toothed. Specimens from moist habitats have darker green and more serrate leaves, while in drier habitats the leaves are nearly entire, paler green, more pubescent, and subcoriaceous in texture. These fluctuations give the specimens a somewhat different

appearance, but they seem to ·be well within the normal range of variation of the species. *A. pallida* differs also from *A. alnifolia* in the fewer-flowered often somewhat corymbiform racemes, usually 15 stamens, the styles 4 or 3 (rarely 5) free nearly to the base, and in the usually smaller fruits.

The forms with darker green, less puberulent, and more serrate leaves that have been described as *Á. gracilis* Heller, and *A. siskiyouensis* Schneider, present at first glance a rather distinctive appearance, and these characters are often more prevalent on plants from higher altitudes, but there is a complete intergradation to the form with pallid, nearly entire leaves, and thus it is scarcely feasible to attempt to maintain more than one species. However, special field work might yield data for possibly varietal separation.

Regarding the Californian serviceberries as varieties of *A. alnifolia* Nutt., Dr. W. L. Jepson (Fl. Calif. 2:234. 1936) noted:

[They are] continuously though not highly variable as to pubescence and leaf shape. Pubescence of the leaves or lack of it, and pubescence of the sepals are not definitely associated with any other character. The leaf-blades are broad, elliptic, or suborbicular and serrate at apex or a little below the apex on the sides. Plants otherwise alike may have puberulent or glabrous leaves . . . In the Coast Ranges and southward to Southern California, the leaf-blades tend to have a few small teeth at apex or are even sometimes entire, though rarely, the teeth may be large or the serrations extend half way to the base. . . . In the Sierra and North Coast Ranges occurs a form (var. *siskiyouensis* Jepson) with oblong or elliptic leaf-blades serrate usually to the middle or nearly to the obtuse base; they are thin at flowering time, weakly puberulent or rarely thinly arachnoid below. . . . On the desert slopes of the Sierra Nevada and the high mountains of Southern California or in ranges bordering the deserts a shrub is found (var. *pallida* Jepson) with elliptic leaves pale or glaucous or whitish pubescent beneath: . . . All these phases, as above indicated, are freely supplemented by intergrades representing many indefinite fractional variations.

Amelanchier alnifolia var. *cuyamacensis* Munz, from Cuyamaca Lake, San Diego Co., and *A. recurvata* Abrams, belong obviously to the same species, and match exactly the typical, or oligodontous, form of *A. pallida* Greene.

18. AMELANCHIER UTAHENSIS Koehne

(Plate III)

Amelanchier utahensis Koehne, Gattung. Pomac. in Wissen. Beil. Progr. Falk.-Real. Berlin 95:25, pl. 2 (1890); Schneider, Illustr. Handb. Laubh. 1:741, figs. 415, 416 (1906); Rydberg, Fl. Rocky Mts. 447 (1917); Tidestrom in Contr. U.S. Nat. Herb. 25:283 (1925); Graham in Ann. Carnegie Mus. 26:233 (1937); Peck, Man. Higher Pl. Oregon 410 (1940); Tidestrom & Kittell, Fl. Ariz. & New Mex. 251 (1941); Kearney & Peebles in U.S. Dept. Agric. Misc. Publ. 423:393 (1942); Abrams, Illustr. Fl. Pac. States, 2:471, fig. 2537 (1944).

Amelanchier alnifolia sensu Coville in Contr. U.S. Nat. Herb. 4:97 (1893), ex p.; Parish in Pl. World 20:217 (1917); I. M. Johnston in ibid. 22:105 (1919). Non Nuttall, 1834.

Amelanchier pallida var. *arguta* Greene in Erythea 1:221 (1893).

Amelanchier alnifolia var. *utahensis* M. E. Jones in Proc. Calif. Acad. Sci. 5:679 (1895).

Amelanchier prunifolia Greene in Pittonia 4:21 (1899); Schneider, Illustr. Handb. Laubh. 1:740, figs. 413, 414 (1906); Rydberg, Fl. Col. 191 (1906); Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909); Rydberg, Fl. Rocky Mts. 447 (1917); E. H. Graham in Ann. Carnegie Mus. 26:232 (1937); Rehder, Man. Cult. Tr. & Shr. 390 (1927), (ed. 2) 389 (1940).

Amelanchier venulosa Greene, in Pittonia 4:21 (1899); Schneider, Illustr. Handb. Laubh. 1:741, fig. 416 (1906); Davidson & Moxley, Fl. S. Calif. 206 (1923).

Amelanchier bakeri Greene in Pittonia 4:128 (1900); Schneider, Illustr. Handb. Laubh. 1:742, fig. 416 (1906); Rydberg, Fl. Colorado 191 (1906); Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909); Wooton & Standley in Contr. U.S. Nat. Herb. 19:323 (1915); Rydberg, Fl. Rocky Mts. 447 (1917); Garrett, Spr. Fl. Wasatch Reg. (ed. 5) 106 (1936); Kearney & Peebles in U.S. Dept. Agric. Misc. Publ. 423:393 (1942).

Amelanchier rubescens Greene in Pittonia 4:128 (1900); Schneider, Illustr. Handb. Laubh. 1:740, figs. 413, 414 (1906); Rydberg, Fl. Colorado 191 (1906); Bean Tr. & Shr. Brit. Isles 1:190 (1914); Wooton & Standley in Contr. U.S. Nat. Herb. 19:322 (1915); Tidestrom in ibid. 25:284 (1925); Tidestrom & Kittell, Fl. Ariz. & N. Mex. 251 (1941).

Amelanchier crenata Greene in Pittonia 4:127 (1900); Schneider, Illustr. Handb. Laubh. 1:742, figs. 415, 416 (1906); Wooton & Standley in Contr. U.S. Nat. Herb. 19:323 (1915); Rydberg, Fl. Rocky Mts. 447 (1917).

Amelanchier rubescens var. *cinerea* Goodding in Bot. Gaz. 37:55 (1904).

Amelanchier elliptica A. Nelson in Bot. Gaz. 40:66 (1905); Rydberg, Fl. Colorado 191 (1906); Schneider, Illustr. Handb. Laubh. 1:739 (1906); Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909).

Amelanchier oreophila A. Nelson in Bot. Gaz. 40:65 (1905); Schneider, Illustr. Handb. Laubh. 1:740, fig. 414 (1906); Rydberg, Fl. Colorado 191 (1906); Coulter & Nelson, New Man. Rocky Mt. Bot. 266 (1909); Wooton & Standley in Contr. U.S. Nat. Herb. 19:323 (1915); Rydberg, Fl. Rocky Mts. 447 (1917); Tidestrom in Contr. U.S. Nat. Herb. 25:283 (1925); Kirkwood, N. Rocky Mt. Tr. & Shr. 189 (1930); Garrett, Spr. Fl. Wasatch Reg. (ed. 5) 106 (1936); Tidestrom & Kittell, Fl. Ariz. & New Mex. 251 (1941); Kearney & Peebles in U.S. Dept. Agric. Misc. Publ. 423:394 (1942).

Amelanchier mormonica Schneider, Illustr. Handb. Laubh. 1:740, fig. 414, n-o (1906), in Fedde, Rep. Sp. Nov. 3:182 (1906); Wooton & Standley, Contr. U.S. Nat. Herb. 19:323 (1915); Rydberg, Fl. Rocky Mts. 447 (1917); Garrett, Spr. Fl. Wasatch Reg. (ed. 5) 106 (1936); Kearney & Peebles in U.S. Dept. Agric. Misc. Publ. 423:394 (1942).

Amelanchier alnifolia var. *elliptica* Schneider, Illustr. Handb. Laubh. 1:739 (1906).

Amelanchier jonesiana Schneider in Fedde, Rep. Sp. Nov. 3:182 (1906); Rydberg, Fl. Rocky Mts. 447 (1917).

Amelanchier goldmanii Wooton & Standley in Contr. U.S. Nat. Herb. 16:131 (1912).

Amelanchier australis Standley in Proc. Biol. Soc. Wash. 26:116 (1913).

Amelanchier covillei Standley in Proc. Biol. Soc. Wash. 27:198 (1914); Wooton & Standley in Contr. U.S. Nat. Herb. 19:323 (1915); Tidestrom in ibid. 25:283 (1925); Abrams, Illustr. Fl. Pac. States, 2:471, fig. 2534 (1944).

Amelanchier purpusi Koehne in Engler, Bot. Jahrb. 52:278 (1915); Rehder, Man. Cult. Tr. & Shr. 391 (1927), (ed. 2) 389 (1940).

Amelanchier plurinervis Koehne in Bot. Jahrb. 52:278 (1915); Rehder, Man. Cult. Tr. & Shr. 391 (1927), (ed. 2) 389 (1940).

Amelanchier nitens Tidestrom in Proc. Biol. Soc. Wash. 36:182 (1923), in Contr. U.S. Nat. Herb. 25:283 (1925).

Amelanchier alnifolia var. *covillei* Jepson, Man. Fl. Pl. Calif. 510 (1925), Fl. Calif.
    2:234 (1936) ; Munz, Man. So. Calif. Bot. 229 (1935).
Amelanchier alnifolia var. *venulosa* Jepson, Man. Fl. Pl. Calif. 510 (1925), Fl.
    Calif. 2:234 (1936) ; Munz, Man. So. Calif. Bot. 229 (1935).
Amelanchier alnifolia var. *nitens* Munz in Bull. So. Calif. Acad. Sci. 31:65 (1932).
Amelanchier utahensis subsp. *covillei* Clokey in Madroño 8:57 (1945).
Amelanchier utahensis subsp. *oreophila* Clokey in ibid. 58.

Shrubs or small trees 0.5-5 m. tall, much-branched, bushy, often grow-
ing in clumps; twigs rigid, the bark ashy gray, those of the season per-
sistently copiously white-sericeous or lanate, rarely nearly or quite gla-
brous, the 2- or 3-year-old twigs also often pubescent; winter buds usually
copiously pubescent, or on occasional specimens glabrous; leaves usually
small, commonly suborbicular to oval, ovate, or obovate, grayish green, or
pale and glaucescent, finely tomentulose or cinereous on both surfaces
even at maturity, with soft, curled trichomes, varying to completely
glabrous, subcoriaceous at maturity, conduplicate in the bud, unfolding
before or with the flowers and more than half-grown at flowering time;
mature blades 0.5-3 cm. long, 0.5-2 cm. wide, the apex rounded or trun-
cate, or even emarginate, or often acute and mucronate, the base rounded
or truncate, or sometimes cuneate; lateral veins 11-13 pairs; margins
coarsely and often sharply dentate to the middle or below varying to
subentire, or crenately few-toothed toward the apex; the teeth mostly 3-5
per cm., 3-10 on each side of average leaves of the flowering and fruiting
branches; stipules linear, pubescent; petioles slender, 5-18 mm. long,
flowers small, sometimes reddish in the bud, in erect or ascending, 3-6-
flowered racemes 2-3 cm. long, sometimes subcorymbose as the result of
the elongation of the lower pedicels; rachis and pedicels lanate (rarely
glabrous), the pubescence usually persistent on the fruiting specimens;
petals 5, white, linear-oblanceolate or cuneate, 6-7 (-9) mm. long, 1.5-2.5
mm. wide; stamens 10-15 (-18), shorter than or equalling the styles, the
filaments glabrous, 1-2 mm. long; anthers 0.7-0.9 mm. long; hypanthium
shallowly campanulate or funnelform, 3-4 mm. in diameter, tomentulose,
varying to completely glabrous, not at all constricted on the young fruit;
sepals linear or linear-lanceolate, acuminate, thickish, tomentulose on both
sides (or occasionally glabrous), 3 mm. long, soon recurved from the
middle and often becoming somewhat elongated after anthesis, or remain-
ing erect or spreading on the fruit; styles 4 or 3, or only 2 (rarely 5),
glabrous, united near the base, 2.5-3 mm. long; summit of the ovary more
or less tomentulose (rarely quite glabrous), tapering into the style-base;
mature fruits few, 6-10 mm. in diameter, 3-6-loculed, usually puberulent
when young, purplish black and juicy at maturity, or often remaining
dry, insipid, pale brown and leathery, and drying on the bush without
ripening; pedicels 2-3 cm. long, usually pubescent; seeds 4-6 in each

pome, brown, microscopically puncticulate, flattened-ellipsoid, obtuse at each end, about 5-6 mm. long and 3 mm. wide when mature and fully developed.

TYPE LOCALITY: "Utah, Belleview [Pintura, Washington Co.], alt. 3000 ped., leg. Marcus E. Jones n. 1716 . . . Vidi in herbario regio Berolinensi." Isotype in the herbarium of the New York Botanical Garden.

RANGE: Dry rocky slopes and canyons, banks of creeks, mountain sides, foothills, and deserts, from the Sonoran to the Transition zones, 4000 to 8000 feet altitude, New Mexico to southern Montana, westward to eastern Oregon and Lower California. Flowering from the beginning of April to the end of May; fruit ripening from July to September, according to the altitude.

OREGON: Vale, Malheur Co., *Leiberg* 2193 (GH); Lake Abert, *Eggleston* 7116 (GH).

IDAHO: Salmon, *Payson & Payson* 1812 (GH); Big Willow, *Macbride* 127 (GH, MBG); King Hill, *Nelson & Macbride* 1110 (GH, MBG); Corral, *Macbride & Payson* 2880a, 2880b (GH, MBG); Soldier Mts., *Macbride & Payson* 2904 (GH, MBG); House Creek, *Nelson & Macbride* 1798 (GH, UI, MBG); Twin Falls, *Nelson & Macbride* 1327, 1347 (GH, MBG); McCammon, *Muenscher & Maguire* 2362 (MBG); Lava, *Nelson & Macbride* 1593 (GH); Montpelier, *Macbride* 13, 24, 209 (GH, UI, MBG).

MONTANA: Wilsall, *Suksdorf* 269 (AA).

WYOMING: Chimney Rock, *Greenman & Greenman* 6031, 6048 (MBG); Telephone Canyon, *Porter* 1059 (MBG); Elk Mt., *Goodding* 555 (AA, GH, MBG); Rawlings, *Payson & Payson* 2540 (GH, MBG); Point of Rocks, *Merrill & Wilcox* 458 (GH); Granger,

MAP 14.—Range of *Amelanchier utahensis.*

Hanna 955 (MBG); Rock Springs, *Hanna* 715 (MBG); Centennial, *Nelson* 9317 (GH), *Jack* 1075, 1089 (AA); Cumberland, *Nelson* 9010 (MBG); near Lyman, *Rollins* 198 (MBG); Mountainview, *Nelson* 11344 (GH); Bear River, *Pammel & Blackwood* 4063 (AA, GH, MBG); Rock River, *Nelson* 9333 (GH, MBG); Bates Hole, *Payson* 4779 (MBG), *Solheim* 434 (UI).

COLORADO: Willow Creek, *Goodding* 1683 (GH, MBG); Camp Creek, *Goodding* 1456 (GH, MBG, ISOTYPE of *A. oreophila*); Rangeley, *Graham* 9074 (GH); Buford, *Hermann* 5688 (GH, MBG); Breckenridge, *Mackenzie* 240 (MBG); Bear Creek, June 13, 1918, *Churchill* (GH, MBG); Golden-Central City, *Duthie & Clokey* 3795 (GH, MBG, UI); White Rocks, May 12, 1918, *Andrews* (AA); near Boulder, *Hanson* C226 (MBG); Mesa Grande, May 1892, *Purpus* (AA); Paonia, *Eggleston* 14572, 14959 (AA), 14574 (GH); Cedaredge, *Payson* 1066 (MBG); Cerro Summit, *Baker* 47, 55, 163 (GH, MBG); near Cimarron, *Baker* 139, 210,

(GH, MBG); Cedar Creek, *Baker* 438, 439 (GH, MBG); Gunnison Mesa, *East-wood* 5095 (AA); Naturita, *Payson & Payson* 3883 (GH, MBG), *Payson* 248 (GH, MBG), *Payson* 982 (MBG); Nuçla, *Payson & Payson* 4225 (GH, MBG); Sheep Creek Canyon, *Payson & Payson* 3884 (GH, MBG); Bedrock, *Payson & Payson* 4228 (GH, MBG); Paradox, *Walker* 210 (GH, MBG); near Ridgway, *Payson* 1077 (MBG), 2307 (GH, MBG); Norwood Hill, *Walker* 416 (GH, MBG); Pagosa Springs, *McKelvey* 4721 (AA); La Veta Pass, *Hooker & Gray* in 1877 (GH); Los Pinos (Bayfield), *Baker* 376 (GH, MBG; ND, TYPE of *A. bakeri*); Durango, *East-wood* 5273 (AA); Bob Creek, *Baker, Earle, & Tracy* 197 (GH, MBG); Mesa Verde Nat. Park, *Munz* 13046 (AA); Mancos, *Baker, Earle, & Tracy* 665 (Minn.; ND, TYPE of *A. prunifolia*).

UTAH: Peterson, *Pammel & Blackwood* 3876 (GH, MBG), 3887 (AA, GH); Goodman Ranch, Bear River Valley, *Hermann* 5813 (MBG); Big Cottonwood Canyon, *Rydberg & Carlton* 6662 (GH); Springville, May 17, 1913, *Hill* (MBG); Red Butte, May 6, 1909, *Clemens* (GH, AA); Salt Lake City, *Palmer* 38037 (AA, MBG); Farmington Canyon, *Pammel & Blackwood* 3623 (GH, AA); Soldier Summit, *Eastwood* 7262, 7263 (AA); Duchesne Co., *Graham* 9407 (GH), 8061, 9284, 9363 (MBG); Green River, *Graham* 9202 (GH), 9196 (MBG); Diamond Mt., *Graham* 8074 (MBG); Ashley Creek, *Graham* 6289 (MBG); near Watson, *Graham* 9006 (MBG); Dry Fork, *Graham* 8810 (MBG); near Vernal, *Graham* 8749 (MBG); Dinosaur Quarry, *Graham* 7659 (MBG); near Helper, *McKelvey* 4267 (AA); Cottonwood Canyon, *Graham* 9519 (MBG); Filmore Forest, *Eggleston* 14164 (GH); Sevier Desert, *Harris* C20491 (GH); Cottonwood Creek, *Cutler* 2372 (MBG); Stansbury Mts., *Harris* C20112 (MBG); Stansbury Island, *Garrett* 5356 (AA); Green Lakes, *Hermann* 4836 (GH, MBG); Uinta Mts., *Williams* 577 (GH, MBG); Milford, *Goodding* 1036 (AA, GH, MBG, ISOTYPES of *A. elliptica*); La Sal Mts., *Purpus* 6523 (MBG), *Maguire & Redd* 1907 (GH); Cooper Canyon, *Cutler* 2297 (MBG); Natural Bridges Nat. Mon., *Maguire & Redd* 1905 (GH); Elk Ridge, *Maguire & Redd* 1911 (MBG); Colorado, *Cutler* 2651 (MBG); Abajo Mts., *Rydberg & Garrett* 9274 (GH); Post Canyon, *Graham* 9896 (GH); Modena, *Goodding* 1008 (AA, GH, MBG); Cedar City, *Tidestrom* 9429 (GH); 50 miles s.w. of San Raphael, *Harrison* 7439 (MBG); Zion Nat. Park, *Allen* in 1934, *Fisk* in 1930 (MBG); Virgin, *Maguire* 4840 (GH, MBG); Rockville, *M. E. Jones* 5224 (MBG); near St. George, *Tidestrom* 9359 (GH), *Goodding* 780 (MBG, TYPE coll. of *A. rubescens* var. *cinerea*); near Glendale, *M. E. Jones* 25393 (MBG), *Nelson & Nelson* 2890 (GH); Belleview, April 21, 1880, *M. E. Jones* 1716 (NY, TYPE coll. of *A. utahensis*).

NEVADA: Hunter Creek, *Kennedy* 1866 (GH, AA); Peavine Mt., *Heller* 9718 (GH); near Alum Creek, *Heller* 9739 (AA); Fish Lake, *Heller* 9995 (AA, GH, MBG), 10004 (AA, GH); W. Humboldt Mts., *Heller* 10630 (GH, MBG); Battle Mts., June 1868, *Watson* 353 (GH); near Cave Creek, *Mason* 4725 (GH), *Heller* 9510 (MBG); Jarbidge, *Nelson & Macbride* 1939 (GH), 1935 (GH, MBG, UI), 2120, 2121 (GH, MBG), *Eggleston* 14105 (GH); near Deeth, *Heller* 10576 (GH, MBG, AA), 10567 (GH), 9108 (AA, MBG), *Eastwood & Howell* 310 (AA), *Maguire* 5772 (GH); Lamoille Creek, *Heller* 9310 (MBG); Oasis, *Palmer* 38025 (AA, MBG); E. Humboldt Mts., Aug. 1868, *Watson* 353 (GH); near Ely, *Tide-strom* 11050 (AA); Carson City, June 2, 1897, *M. E. Jones* (MBG); Kings Canyon, *Baker* 946 (AA, GH, MBG); Glenbrook, *Baker* 1002 (AA, GH, MBG); White Mts., *Duran* 752 (GH, MBG); near Panaca, *Tidestrom* 9460 (AA); Kyle Canyon, Charleston Mts., *Tidestrom* 9600 (GH), *Clokey* 7141, 7142 (GH), 7541, 7542 (GH, MBG, UI); Wilson's Ranch, Charleston Mts., Clark Co., *Clokey* 7970 (GH), 8236, 8237 (GH, UI), TOPOTYPES of *A. nitens;* Wells, July, 1893, *E. L. Greene* (ND, TYPE of *A. pallida* var. *arguta*).

CALIFORNIA: Portola, *Eastwood* 7017 (AA); Providence Mts., *Munz, et al.* 4147 (GH); Panamint Mts., *Munz* 14820 (MBG); Argus Peak, *Purpus* 5376 (GH, MBG); Old Dad Mts., *M. E. Jones* 25392 (MBG); Wrightwood, *Newsom* in 1932 (GH, MBG); Cushenberry Springs, Bear Valley, San Bernardina Mts., *Parish*

453, 3383 (MBG), 1290 (GH, TYPE coll. of *A. venulosa*), 10882 (GH, MBG); Bear Valley, *Abrams* 2884 (GH, MBG); Deep Creek, *Abrams* 2041 (AA); Sugarloaf Peak, *Fosberg* 8605 (GH); San Antonia Peak, *M. E. Jones* 29011 (MBG), *Parish* 11969 (GH, MBG); Laguna Mts., *Eastwood* 9212 (AA).

ARIZONA: Peach Springs, *Wilson* in 1893 (GH); Grand Canyon, *Rehder* 115, 116 (AA), *Eastwood* 5886, 5948 (AA), *Nelson & Nelson* 2024 (MBG); *McKelvey* 4395 (AA), *Eastwood* 6047, 6086 (AA, GH); between House Rock and Jacob Lake, *Nelson & Nelson* 2877 (GH, MBG); 7 miles northwest of Jacobs Lake, *Peebles & Parker* 14670 (GH); 18 miles north of Inscription House Trading Post, *Peebles* 13920 (GH); Mormon Lake, *Smith* 12005, *MacDougal* 102 (GH, TYPE coll. of *A. mormonica*); Kendrick Peak, June 22, 1911, *Lowell* (AA); near Flagstaff, *McKelvey* 1314 (AA), *Lowell* in 1915 (MBG), *Hanson* 626 (MBG); Williams, *Nelson* 10245 (MBG); between Williams and Ash Fork, *McKelvey* 915 (AA); Mt. Agassiz, May 1916, *Pearson* (AA); between Tunitcha and Luka-Chukai Mts., *Goodman & Payson* 2797, 2846 (MBG); Navajo Indian Reservation, *Voorhies* 82 (GH, AA, MBG); Matazal Mts., *McKelvey* 1034, 1138 (AA), *Collom* 488 (MBG); Verde R., between Payson and Pine, *McKelvey* (AA); Devils Canyon, between Miami and Superior, *Nelson & Nelson* 1888 (MBG); Camp Grant, *E. Palmer* 94 (MBG).

NEW MEXICO: Above Toadlena, *McKelvey* 4626, 4630 (AA); Aztec, *Baker* 377 (GH, AA, MBG, TYPE coll. of *A. crenata*), *Baker* 380, 381 (GH, MBG; ND, TYPE of *A. rubescens*); Chama, *Wolf* 2988 (GH); Lake Burford, *Wetmore* 470 (AA); Tierra Amarilla, *Eggleston* 6575 (GH, MBG); near Gallup, *McKelvey* 2316, *Eastwood* 5609 (AA); Pecos River, 8 miles east of Glorietta, *Heller* 3679 (AA, GH, MBG); Winsor Creek, *Standley* 4125 (GH, MBG); Mogollon Mts., Aug. 8, 1900, *Wooton* (MBG); Kingston, *Metcalfe* 961 (GH, MBG); near Silver City, *Greene* in 1880 (MBG), *Metcalfe* 620 (GH, MBG).

TEXAS: Ridge above McKittrick Canyon, Guadalupe Mts., *Moore & Steyermark* 3482 (GH, MBG).

MEXICO: San Pedro Mártin, Baja California, May 26, 1893, *Wiggins & Demaree* 4948 (FM, UC), *T. S. Brandegee* (UC).

This common Amelanchier, occurring throughout the mountainous and desert regions of western United States, is an extremely variable species, for which the oldest name is *A. utahensis* Koehne, applied in 1890 to specimens collected near the geographical center of its range, in southwestern Utah. Its variability is indicated by the fact that during the half-century that has elapsed since this species was first recognized, it has been described and redescribed under approximately two dozen different names. In its typical form, it is a twiggy shrub with rather small, permanently pubescent, conspicuously toothed leaves that are subcoriaceous at maturity. The branchlets may be pubescent for two or three years. Shade forms have larger, thinner leaves, and tend to approach *A. alnifolia* in general appearance, but such specimens can usually be distinguished by the fewer styles and stamens, and the narrower, often somewhat elongated sepals. One of the vernacular names used for this species is "red serviceberry," because in some localities the flower buds are pink. It is sometimes abundant locally, and is said to be palatable as a browse plant in the spring.

An Amelanchier inhabiting the arid slopes and plains of parts of southern California, including shrubs with rather prominently veiny

leaves, was described by E. L. Greene in 1899 as *A. venulosa*. However, it lacks morphological characters to distinguish it from *A. utahensis*. Greene recognized the fact that it is different from *A. pallida* in its more venulose leaves, but was apparently unaware that it had been published as *A. utahensis* nine years earlier. The specimens described as *A. rubescens* Greene, collected "In arroyos and among hills about Aztec, New Mexico, 24 April 1899, C. F. Baker" (nos. 380, 381), are also clearly conspecific with *A. utahensis*. Likewise, *A. crenata* Greene, also from Aztec, New Mexico, and said by its author to be "altogether peculiar in the crenate character of its leaf indentation" is merely a phase of the widespread and variable *A. utahensis*. The plants described as *A. rubescens* var. *cinerea* by L. N. Goodding in 1904 from near the type locality of *A. utahensis*, represent merely a pubescent extreme of that species. *A. plurinervis* Koehne was described from plants cultivated in Berlin, but collected by C. A. Purpus in western United States. Specimens distributed from Arb. Spaeth., now in the herbarium of the Arnold Arboretum, belong quite evidently to *A. utahensis*.

In 1905, Professor Aven Nelson, concluding that "either *A. alnifolia* was unusually variable or that some segregation ought to be made," described the common western xerophytic shrub with puberulent leaves, fewer styles and stamens, and smaller fruits, as *A. oreophila*, apparently without knowing that this species had been described as *A. utahensis*, from southwestern Utah fifteen years earlier by E. Koehne. Nelson's comments in Bot. Gaz. 40:66 (1895) are as follows:

> After many years' observation in the field and the study of a large series of specimens, I am satisfied that two valid species exist and can be readily distinguished. Nuttall's *A. alnifolia* is the widely distributed glabrous shrub of the creek banks, moist canyons, and snow slopes. . . . The leaves are larger, coarsely serrate, often suborbicular or with a tendency to truncateness at base and apex. . . . The fruits become much larger, are purple, with bloom, juicy and well flavored, and are used extensively for sauces and pies, maturing during July or August, according to the altitude. *A. oreophila* [*A. utahensis*] is a smaller shrub, scraggy-branched, usually in dense clumps, and occurring in the driest situations (open stony slopes, ridges, and hilltops). It is never wholly glabrous, and the fruit is of little if any value. . . . Much of the material distributed from the Rocky Mountains belongs to this species.

In 1923, Dr. Ivar Tidestrom described, as *A. nitens*, a glabrous shrub with glossy foliage and yellow fruits occurring in the Charleston Mountains of southwestern Nevada. In its extreme glabrous form, this is a plant of distinctive appearance, but it intergrades completely with the typically pubescent forms of the widespread *A. utahensis*, and it is therefore not practicable to attempt to accord it nomenclatural recognition. Even on topotypes collected in 1938 and 1939 by Mr. I. W. Clokey (e.g., *Clokey* 8236, 8237, UI) some specimens are almost perfectly glabrous,

while others are distinctly pubescent on the blades, petioles, pedicels and sepals. This glabrous or semi-glabrous form has no particular geographical distribution, but occurs sporadically in various intergrades, in several parts of the range of *A. utahensis.* Dr. Rogers McVaugh[1] reports his field observations of these plants as follows:

In desert and semi-desert areas from Clark Co., Nevada, throughout the Grand Canyon region, there is an abundance of a glabrous or nearly glabrous form with small lustrous leaves, which seems to be otherwise identical with Form C [i.e., *A. utahensis*]. This is the plant described as *A. nitens* Tidestrom, which was said by its author to have yellow fruit ("pomis maturis aureis"). In July 1941 I was able to visit Wilson's Ranch, the type locality of this species, and to collect mature fruits. As in many similar localities in the southern Great Basin, most of the fruits had dried at maturity, leaving the seeds to rattle within. On a few bushes, however, I was able to find an occasional berry [pome] which was still soft and slightly fleshy; all these were pale, nearly white, with a purplish-red cheek; they were in fact identical with the fruits of *A. utahensis* from other parts of its range.

There seems to be no evidence that yellow or orange fruits, usually ascribed to certain western American species, ever actually occur, except perhaps as a result of the attacks of fungous diseases. In drier habitats, it commonly happens that the fruits are small, dry and leathery. Frequently they never ripen, or when they do ripen they remain on the bush and retain a pale brown leathery appearance. Several rust fungi, particularly *Gymnosporangium,* parasitize various species of Amelanchier. It may be that fruits heavily infected with this fungus, which gives them a yellowish appearance, have been the cause of the widespread misconception regarding the color of the fruit of some western species. The fruits of all species of Amelanchier are normally bluish black at maturity.

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[1]McVaugh, Rogers, Contributions Toward a Flora of Nevada, No. 22, pp. 95-96, June 15, 1942. Issued (mimeographed) by The Division of Plant Exploration and Introduction, Bureau of Plant Industry, U.S. Department of Agriculture, Washington, D.C.

Abbe, E. C.—1136, 1151 (1).

Abrams, LeRoy—2041, 2884 (18); 3912, 4577, 4675, 4809, 4817, 5577 (17); 8718 (13).

Abrams, LeRoy, & McGregor, E. A.—107, 490 (17).

Adams, J.—339 (7).

Adams, J., & Wherry, E. T.—4662 (6).

Aiton, G. B.—1004 (9).

Allard, H. A.—220, 2516, 2584, 2819, 4342, 4498 (6); 4353 (5); 1229 (7).

Allen, O. D.—214 (13).

Anderson, E., & Anderson, D. M.—26042 (11).

Applegate, E. I.—6219 (12).

Arsène, L.—310 (5); 311 (1).

Arthur, J. C., Bailey, L. H., & Holway, E. W. D.—B407 (1).

Bacigalupi, R.—1549 (17).

Bailey, L. H.—56 (11).

Baker, C. F.—47, 55, 139, 163, 210, 376, 377, 380, 381, 438, 439, 946, 1002 (18); 49, 379 (16); 750 (12); 952, 1219, 2964 (17).

Baker, C. F., Earle, F. S., & Tracy, S. M.—197, 665 (18).

Balser, G.—775 (9).

Barber, M. A.—90, 194 (12).

Barkley, F. A., & Osburnson, L. — 2313 (14).

Bartlett, H. H.—846 (9).

Bartram, E. B.—3220 (8).

Batchelder, C. F.—3 (5).

Bates, J. M.—5992 (6); 1357, 5928, 6074 (12).

Bean, R. C., & Fernald, M. L.—17013, 17014 (9).

Bean, R. C., & Knowlton, C. H.—12070e (10).

Bean, R. C., White, D., & Linder, D. H. —21459 (1).

Beattie, R. K.—1819 (12).

Benner, W. M.—4883 (6); 6708 (4); 2393, 9567 (5); 2703 (8); 2926, 7533 (9).

Benson, L.—1283 (14); 1420, 1423 (13a).

Bergman, H. F.—1376 (9).

Bicknell, E. P.—4835 (5); 4815, 4816, 4840, 4847, 4849, 4850, 4851, 4857, 4858, 4862a, 4868, 4879 (7).

Biltmore Herbarium—5664, 5664c, 5664d, 5664e (10); 6706 (9).

Bishop, H.—370, 371, 373 (1).

Bissell, C. H., & Graves, C. B.—21457 (7).

Bissell, C. H., Pease, A. S., Long, B., & Linder, D. H.—21440 (7).

Blake, S. F.—2496, 5677 (9); 9324, 9362 (7); 10557 (6).

Blake, S. F., & Fernald, M. L.—3645 (9).

Blanchard, W. H.—3, 4 (9); 4 (10); 5 (1).

Blankinship, J. W.—135 (12).

Blewitt, A. E.—1508, 1801 (7); 1511, 1792, 1794, 1795, 1796, 2035, 2037 (9); 1512, 1797, 1798 (5); 1802, 1804, 1805, 2036, 2038, 2039, 3501, 3650 (6).

Bolander, H.—4674 (13).

Boner, L., & Weldert, V.—172 (14).

Bowman, P. W.—26, 237, 402 (1).

Breckenridge, W. J., & Nielsen, E. L.—3161 (4).

Breckenridge, W. J., Nielsen, E. L., & Moore, J. W.—3229 (4).

Breitung, A. J.—523 (12).

Brewer, W. H.—576 (17).

Brown, H. E.—78 (12); 557 (17).

Brown, S.—23, 56 (12); 216 (9); 283 (13).

Burnham, S. H.—11 (7); 12 (5); 21 (3); 1162 (6).

Bush, B. F.—30, 85, 85a, 85b, 85c, 1602, 1602a, 3509, 10380, 15250 (6).

Butters, F. K.—1342 (4).

Butters, F. K., & Rosendahl, C. O.—1358 (12).

Byhouwer, J. T. P., & Kobuski, C. E.—50 (7).

Carr, W. P.—75 (12).

Chamberlain, E. B.—34, 52, 533 (5); 62, 228 (9).

Chandler, H. P.—1282 (17).

Chase, Agnes—197, 1047 (5); 702, 709, 990, 1048, 1745 (9); 2035, 2053 (6).

Chase, V. H.—1795 (6).

Cheney, L. S.—4447 (4).

Child, H. W., Knowlton, C. H., Bird, F. W., & Bean, R. C.—16377 (5).

Clark, J. A.—166 (12).

Clokey, I. W.—7141, 7142, 7541, 7542, 7970, 8236, 8237 (18).

Collom, R. E.—488 (18).

Congdon, J. W.—31 (17).

Constance, L.—999 (14).

Constance, L., Clements, H. F., & Machlis, L.—1008 (14).

Constance, L., Machlis, L., Rogers, B., & Rollins, R. C.—1037 (14).

Constance, L., & McMurray, R. L.—1135 (12).

Constance, L., & Rollins, R. C.—1510 (12) ; 1499, 1512 (14).

Constance, L., Rollins, R. C., & Dillon, L. A.—1568 (15).

Cooper, W. S.—46 (1) ; 122, 124, 125 (11).

Cotton, J. S.—365, 569, 571, 576 (12).

Cowles, H. C.—38, 38a (12) ; 1419 (13).

Cronquist, A.—920, 2298, 3778 (12) ; 2596 (16).

Cronquist, A., & Davis, R. J.—2099 (12).

Culbertson—4647 (17).

Cushman, J. A.—871, 4330 (10).

Cushman, J. A., & Sanford, S. N. F.—1217 (3).

Cusick, W. C.—1858 (14).

Cuthbert, A.—1 (7).

Cutler, H. C.—2297, 2372, 2651 (18).

Daniels, F.—909 (16).

Davis, J.—49, 113, 704, 1259, 1462, 2011, 2227, 4646 (6).

Day, M. A.—57, 75 (7) ; 379 (3).

Deam, C. C.—12868, 16116, 33798 (5) ; 22524, 23005 (6) ; 23107, 33770, 38194, 38195, 38196, 38251, 39083 (9).

Demaree, D.—11245, 11260, 18743 (6).

Dodge, C. K.—20, 57, 71, 73 (8) ; 74, 76 (10).

Drew, W. B., Hodgdon, A. R., & Taylor, F.—2472 (10).

Drouet, F.—1421 (6).

Dudley, W. R.—56 (7).

Dunbar, J.—10 (9) ; 12 (10).

Duncan, W. H.—3282 (5).

Duran, V.—752 (18).

Duthie, R., & Clokey, I. W.—3795 (18).

Eames, A. J., & Dean, E.—4293 (6).

Eames, A. J., & MacDaniels, L. H.—4285 (9).

Eames, E. H.—1 (5) ; 4287, 4288 (9) ; 8287 (6).

Earle, F. S., & Baker, C. F.—1610 (6a).

Eastwood, A.—72, 785, 1081, 11931, 12076 (17) ; 269, 7706 (12) ; 372 (16) ; 995, 9702 (13) ; 5095, 5273, 5609, 5886, 5948, 6047, 6086, 7017, 7262, 7263, 9212 (18).

Eastwood, A., & Howell, J. T.—310 (18) ; 4800 (17).

Eggleston, W. W.—185, 1176, 1179, 1180 (9) ; 1118, 1173, 1174, 1175 (3) ; 1121, 1122, 1127, 1178, 1971 (10) ; 1182,

Eggleston, W. W. (*continued*) 1183, 1957, 1959 (6) ; 1960, 1962, 1964, 2369 (1) ; 6235, 7596 (17) ; 7066 (16) ; 6575, 7116, 14105, 14164, 14572, 14574, 14959 (18) ; 14967 (12).

Ehlers, J. H.—323 (10) ; 1183 (9).

Elmer, A. D. E.—135 (14) ; 2512 (13) ; 4659 (17).

Epling, C.—5623 (13).

Evers, R. A.—52 (6).

Eyerdam, W.—1377 (14).

Eyles, D.—6894 (6).

Farwell, O. A.—52d (1).

Fassett, N. C.—446, 2826, 13745 (5) ; 2818, 2819, 2820, 2821, 2822, 2823, 13775 (9) ; 2825, 3051, 7128 (4) ; 7313 (10).

Fassett, N. C., & Schmidt, J. F. W.—15708 (9).

Fassett, N. C., Steyermark, J. A., & Tryon, R. M.—18359 (9).

Fernald, G. B.—43 (9).

Fernald, M. L.—37, 2312, 11719 (3) ; 105, 1881, 1888, 2644, 9620, 9626, 13760, 13773, 13774, 13775, 15197, 15204, 16867 (9) ; 257, 2314 (1) ; 9624 (5) ; 388, 449, 1880, 2310, 2311, 13778, 13779, 15537 (10) ; 1885, 13767 (6) ; 15191, 15198, 15199, 18546 (7).

Fernald, M. L., Bartram, E. B., & Long, B.—23930, 23931 (9) ; 23937 (7) ; 23943, 23944, 24761 (5).

Fernald, M. L., Bartram, E. B., Long, B., & Fassett, N. C.—23929 (9).

Fernald, M. L., Bartram, E. B., Long, B., & St. John, H.—7553, 7582, 7591 (9) ; 7581 (3) ; 7586, 7587, 7589 (2).

Fernald, M. L., & Bean, R. C. — 14132 (9) ; 14160 (7).

Fernald, M. L., & Bissell, C. H.—21433 (9).

Fernald, M. L., Bissell, C. H., Graves, C. B., Long, B., & Linder, D. H.—21441, 21442 (5).

Fernald, M. L., Bissell, C. H., Pease, A. S., Long, B., & Linder, D. H.—21432 (9).

Fernald, M. L., & Collins, J. F.—233, 614, 1100 (1).

Fernald, M. L., Dodge, C. W., & Smith, L. B.—25840 (11).

Fernald, M. L., & Griscom, L.—4425 (6).

Fernald, M. L., Griscom, L., & Long, B. —4650 (6).

Fernald, M. L., Griscom, L., Mackenzie, K. K., & Smith, L. B.—25839 (11).

Fernald, M. L., & Hunnewell, F. W.—
15192 (5); 15200 (7).

Fernald, M. L., & Jackson, H. B.—10107
(1).

Fernald, M. L., & Long, B.—3959, 7063,
7064, 7065, 7067, 7069, 7450, 8291,
9621, 11698, 11844, 11845, 13039, 13040,
13041 (6); 7068, 7070, 7071, 7869,
9625, 9949, 11343, 12096, 13772, 16869,
18542, 18543, 23946 (7); 7072, 7073,
7074, 7448, 7449, 7870, 9947, 11846,
11847, 13042, 13043, 13950 (8); 9623,
13763, 21451 (5); 13762, 13766, 13777,
13781, 14178, 18548, 18549, 18551,
23932, 23933, 23934 (9); 13764, 13768,
13769, 21450 (3); 13780 (10); 13782
(1).

Fernald, M. L., Long, B., & Dunbar,
B. H.—26759 (9).

Fernald, M. L., Long, B., & Fogg, J. M.
—290, 1791 (5); 292, 1789 (1); 1792
(2).

Fernald, M. L., Long, B., & Linder,
D. H.—21439 (9); 21456 (7).

Fernald, M. L., Long, B., & St. John, H.
—7584, 7593, 7594, 7595 (9); 7590,
7592 (2); 7596, 7597 (1).

Fernald, M. L., Long, B., & Smart,
R. F.—5790 (8).

Fernald, M. L., & Pease, A. S.—3359,
25134 (9); 3360, 25133 (1); 3361,
3364, 3365, 3366, 3367 (10); 3369,
25137 (11); 16825 (3); 25135 (5).

Fernald, M. L., Pease, A. S., &
Long, B.—11700 (7); 21435, 21436,
21437 (9).

Fernald, M. L., & St. John, H.—7578
(3); 7585, 11080 (9); 10840, 10841,
10842, 11083 (2); 11082 (5); 11085
(7).

Fernald, M. L., & Smiley, F. J.—11720
(1).

Fernald, M. L., & Svenson, H. K.—914
(9).

Fernald, M. L., Weatherby, C. A., &
Stebbins, G. L.—2451 (11).

Fernald, M. L., & White, D.—21438 (9).

Fernald, M. L., & Wiegand, K. M.—
3554, 5535, 5574, 5574a, 5576, 5578,
5597, 5600, 5602, 5736, 5737, 5738,
5739, 5742, 5743, 5744, 5745, 5746,
5748, 5749, 5750, 5751, 5752, 5754,
5755, 5756, (1?); 5542, 5545, 5547,
5552, 5567, 5568, 5569, 5570, 5578a,
5580, 5599, 5755 (5); 3553, 5557, 5565,
5558, 5559, 5561, 5562, 5563, 5605,
5608, 5623, 5627, 5630, 5633, 5635 (9).

Fernald, M. L., Wiegand, K. M., &
Eames, A. J.—14302 (10).

Ferris, R. S., & Duthie, R.—77 (17);
411, 784 (12); 656 (15).

Fischbach, C. M.—228 (6).

Flodman, J. H.—545 (16).

Floyd, F. G.—801, 803, 980, 1008 (9);
845 (5).

Fogg, J. M.—1863, 4049, 16324 (9).

Fosberg, F. R.—8605 (18).

Friesner, R. C.—9541 (6).

Garrett, A. O.—3686 (12); 5356 (18).

Gates, F. C., & Gates, M. T.—9544,
13914 (10).

Geil, D.—4 (14).

Gilbert, F. A.—398 (7).

Gilbert, F. A., Rehder, A., & Smith,
L. B.—833 (7).

Gleason, H. A.—708 (5); 1695, 2404 (6).

Godfrey, R. K., & White, R. N.—7027
(9).

Godfrey, R. K., White, R. N., & Shel-
bourne, V.—7038 (7).

Goodale, A. S., & Markert, W. C.—
76864 (9).

Goodding, L. N.—555, 780, 1008, 1036,
1456, 1683 (18).

Goodman, G. J., & Payson, L. B.—2797,
2846 (18).

Gorman, M. W.—39 (13); 1026 (12).

Graham, E. H.—6289, 7659, 8061, 8074,
8749, 8810, 9006, 9074, 9196, 9202, 9284,
9363, 9407, 9519, 9896 (18); 9262
(12).

Grant, M. L.—2862 (4).

Greene, E. L.—779 (17).

Greenman, J. M.—936, 1058 (1); 3024
(9).

Greenman, J. M., & Greenman, M. T.—
6031, 6048 (18).

Greenman, J. M., Lansing, O. E., &
Dixon, R. A.—81 (6).

Grimes, E. J.—2560 (6).

Griscom, L.—21578 (6).

Hanna, L.—715, 955 (18).

Hansen, G.—230 (17).

Hanson, H. C.—C225 (12); C226, 626
(18).

Harbison, G. J.—1, 9, 30, 194, 813, 846,
7236, 7240 (9); 2, 510, 913 (5); 4, 6,
11, 15, 30, 40, 1415, 7095 (6); 8 (7).

Harger, E. B.—3, 10 (5).

Harper, R. M.—819 (7); 1806 (6);
3322 (6a).

Harris, J. A.—C20112, C20491 (18);
C28699 (16).

Harris, S. K.—423 (7).

Harris, S. K., & Pease, A. S.—26551 (3).

Harrison, B. F.—7439 (18); 7473 (12).

Harrison, B. F., & Larsen, E. — 7685 (16); 7877 (12).

Hay, G.—63 (1).

Hayden, A.—10489 (9).

Heller, A. A.—2988 (15); 3679, 9108, 9310, 9510, 9718, 9739, 9995, 10004, 10567, 10576, 10630 (18); 3061, 3679, 9739 (12); 3958 (13); 5794, 5961, 6617, 7038, 7419, 7970, 8003, 8531, 10875, 11963, 12729, 12962, 13004, 13156, 13396, 15144 (17); 7176 (16).

Henderson, L. F.—5147 (14); 5824, 13004 (17).

Hermann, F. J.—4836, 5688, 5813 (18); 6471, 7259, 10191 (5); 6486, 6497 (9); 4016, 9625 (6); 7791 (10); 10048 (7).

Herriot, W.—72329 (12).

Hill, A. F.—169 (16); 1614 (3); 1700 (9).

Hill, E. J.—231895 (9); 321889 (5); 411912 (6).

Hitchcock, C. L.—2290 (12); 6701 (17).

Hodgdon, A. R.—195, 2244, 2245 (5); 2471, 2998 (10); 2600, 2845, 3192 (9); 2597, 2773 (7).

Hodgdon, A. R., & Dunn, S.—2772 (5).

Horner, R. M.—B183 (14).

Horsey, R. E.—323 (6).

Hotchkiss, N.—2290 (1).

House, H. D.—7264, 9468, 10227 (1); 7265, 8943, 10175, 17246 (9); 7787, 11870 (6); 7961 (5); 10189 (3); 11201, 16059 (10).

Howe, C. D., & Lang, W. F.—265, 297 (5); 1081, 1203 (1).

Howell, T.—1132 (13).

Hubbard, F. T., & Torrey, G. S.—T352 (9).

Hubricht, L.—B2011 (6).

Hughes, J. A.—1185 (14).

Hunnewell, F. W.—4029, 4128, 6889 (6); 4129, 5885 (5); 4681 (10); 5895 (9); 6031 (7); 2445, 6169 (12).

Hunnewell, F. W., & Wiegand, K. M.—2137, 2139, 2140, 2143 (7).

Hunt, K. W.—2969 (8).

Hunt, K. W., & Martin, F.—1408, 2526 (8).

Hyland, F.—699, 753 (7).

Jack, J. G.—628, 680, 3187, 3188, 3648, 3671 (5); 684, 3108, 3583, 3639, 3948 (7); 1075, 1089 (18); 1051, 1124a, 1125, 1155, 1185, 1213, 1258, 1336,

Jack, J. G. (continued)
1359, 1361, 1374, 1379, 1453, 1497, 1498, 1511, 1537, 1580, 1592, 2007, 2293, 2540, 2629, 2778 (12); 2865 (13); 3106, 3344 (1); 3209, 3357, 3479, 3514, 3762, 3872, 3946 (9); 3928 (10).

Jenney, C. F., Churchill, J. R., & Hill, A. F.—3264 (6).

Jennings, O. E.—1581 (7); 14015 (1); 14024c (11); 14521 (9).

Jones, G. N.—972, 7137 (15); 1397, 2057, 4681, 5084, 5640 (12); 4565, 5819 (13a); 1387, 1398, 2832, 6349, 6573, 7088, 7101, 7134, 7147 (14); 7690, 7755 (17); 11992, 12089, 13143, 13340, 15618, 15840 (6); 17143 (9).

Jones, G. N., & Jones, F. F.—13716, 13750, 13781, 15323 (5); 16170 (1).

Jones, M. E.—1716, 5224, 29011, 25392, 25393 (18); 1447, 6274, 25397 (12).

Kennedy, G. G.—17, 257 (1); 1866 (18); 2360, 3260 (7).

Kimball, R. H.—102 (1).

Kirkwood, J. E.—28, 29, 30, 1182 (14).

Koehler, H. J.—1 (9); 2 (5).

Kraus, E. J.—16, 22 (10).

Krotkov, P. V.—5384, 5390 (10); 7517 (9).

Lakela, O.—2873 (9).

Lamb, F. H.—1190 (13a).

Leiberg, J. B.—1203 (12); 2193 (18).

Letterman, C. W.—2, 3 (6).

Long, B.—6633, 8476, 12515, 12867, 14522, 16257, 18378, 21447, 21448, 30691, 32022, 32349, 33631, 41781, 48444, 50001, 52074, 54418, 57028 (5); 3107, 6586, 9610, 11605, 11883, 11943, 13516, 14514, 14519, 32089, 32282, 37298, 37719, 46255, 46808, 50133, 51868, 52160, 52340, 53736, 58228 (6); 26820, 31233, 32689, 33309, 33330, 33615, 34224, 54350, 57005, 57021, 58240 (7); 5915, 16451, 18759, 21005, 21590, 30300, 30603, 30773, 32883, 33071, 35296, 45720, 48268, 48766, 52012, 54322, 54368, 54423, 58269 (8); 12504, 12556, 20586, 25839, 30640, 32642, 37315, 48649, 51076, 51838, 52017, 52022, 52088, 52094, 56467 (9).

Long, B., & Pennell, F. W.—7364, 7374 (8).

Long, B., & St. John, H.—2479 (6).

Long, C. A. E.—320, 335, 852 (9).

Loomis, J. A.—856 (9).

Louis-Marie, Fr.—116 (9); 145 (5).

Lucy, T. F.—818b (9).

Lunell, J.—50 (14).

Macbride, J. F.—13, 24, 127, 209 (17) ;
    852 (14) ; 926 (12).
Macbride, J. F., & Payson, E. B.—2880
    (16) ; 2880a, 2880b, 2904 (18).
MacDougal, D. T.—102 (18) ; 178 (12).
Mackenzie, K. K.—240 (18) ; 3080, 4201
    (9).
Mackenzie, K. K., & Griscom, L.—5804
    (10) ; 10327 (1) ; 11102 (5).
MacMillan, C., & Sheldon, E. P.—1747a
    (10).
Macoun, J.—208 (13a) ; 12627 (12) ;
    79796, 93380, 93875, 93879, 93880,
    93881, 93883, 93887, 93889, 93895,
    93897, 93898, 93899, 93901 (13) ; 19043
    (5) ; 66927 (3) ; 20074 (10) ; 34296
    (6) ; 34298, 34301, 66924, 80733, 85506
    (9).
Macoun, J. M., & Malte, M. O.—88016
    (5).
Maguire, B.—2363, 3501, 3507 (12) ;
    4840, 5772 (18).
Maguire, B., & Redd, J. D.—1905, 1907,
    1911 (18).
Manning, W. E., & Seymour, F. C.—
    3687 (9).
Marie-Victorin, Fr.—11222, 15586, 24546,
    24547 (6) ; 1883, 11216, 18715 (10) ;
    2087, 8237, 9504, 11221, 11223, 15585,
    24545, 24548 (9) ; 4318 (2) ; 4319,
    9503, 11219 (5) ; 11214, 15589 (1) ;
    24538, 24558, 28582, 28694 (11).
Marie-Victorin, Fr., Brunel, J. B., Rol-
    land-Germain, Fr., & Rousseau, Z.—
    17433, 17436 (1) ; 17431, 17434,
    17435 (11).
Marie-Victorin, Fr., & Rolland-Germain,
    Fr.—9507, 18710, 18711, 27898, 27900
    (2) ; 18707, 18708, 18709, 27899, 27901
    (1) ; 33110, 33130 (9).
Marie-Victorin, Fr., Rolland-Germain,
    Fr., & Jacques, E.—33203, 33298,
    33440 (11) ; 33216, 33436, 33439 (2) ;
    33467, 33486 (1).
Marsh, V. L.—507 (12).
Mason, H. L.—4725 (18).
Mattioli, A. & E.—7, 13, 20 (4).
Mattoon, E. A.—13 (6).
McFarland, F. T.—18 (5).
McKelvey, S. D.—915, 1034, 1138, 1314,
    2316, 4267, 4395, 4626, 4630, 4721 (18).
Menzel, R. W.—403 (7).
Merrill, E. D., & Wilcox, E. N.—458
    (18) ; 548 (16) ; 1027a (12).
Merrill, G. M.—1965 (6).
Metcalfe, O. B.—620, 961 (18).
Meyer, F. G.—226 (15) ; 854, 1428 (14).

Milburge, Sister M.—258 (14).
Moffatt, W. S.—190 (6) ; 1610 (9).
Moldenke, H. N.—9502 (5) ; 10580 (7).
Moodie, M. E.—817, 1039 (12).
Moore, A. H.—4189 (3).
Moore, J. A., & Steyermark, J. A.—
    3482 (18).
Moore, J. W., & Nielsen, E. L.—3653
    (4).
Morton, J. A.—2691 (1).
Moyle, J. B.—216 (9).
Moyle, J. B., & Nielsen, E. L.—1944
    (4).
Muenscher, W. C.—50 (7) ; 9635, 15136
    (13) ; 11427, 11485 (12).
Muenscher, W. C., & Clausen, R. T.—
    4020 (1).
Muenscher, W. C., & Maguire, B.—2319,
    2320 (3) ; 2322 (9) ; 2360 (12) ; 2362
    (18).
Muenscher, W. C., & Spalteholz, R.—
    16175 (7).
Muenscher, W. C., Wilson, C. L., &
    Foster, A. S.—15609 (9).
Mulford, A. I.—192 (16).
Munz, P. A.—8099 (17) ; 13046, 14820
    (18).
Munz, P. A., & Johnston, I. M.—12638
    (17).
Munz, P. A., Johnston, I. M., & Har-
    wood, R. D.—4147 (18).
Murdoch, J.—4035 (12).
Murdoch, J., & Torrey, G. S.—T391 (9).
Murie, O. E.—1122 (13a) ; 1183 (12).
Myers, J. C.—415 (6).

Nelson, A. — 1931 (16) ; 2129, 10086,
    10530 (12) ; 9010, 9317, 9333, 10245,
    11344 (18).
Nelson, A., & Macbride, J. F.—1052,
    1273, 1405, 1593, 1847 (12) ; 1110,
    1327, 1347, 1593, 1798, 1935, 1939,
    2120, 2121 (18) ; 1368 (16).
Nelson, A., & Nelson, R.—783, 798 (12) ;
    1888, 2024, 2877, 2890 (18).
Nelson, E.—807 (12).
Nelson, J. C.—1071 (13) ; 1475 (17).
Newins, H. S.—8141 (5).
Nichols, G. E.—168, 557 (5).
Nielsen, E. L.—1055, 1060, 1063, 1064,
    1066, 1069, 1082, 1091, 1301, 1376,
    1379, 1804, 1820, 1931, 2485, 2521,
    2547, 2669, 2961, 3113, 3124, 3127,
    3129, 3131, 3133, 3136, 3137, 3138,
    3170 (4) ; 1868, 1872 (5) ; 1630 (6) ;
    1349, 1967, 2500 (10).

Ownbey, M.—593 (12).

Packard, J.—371 (14).

Palmer, E.—94 (18).

Palmer, E. J.—1602, 5616, 14684, 20761, 20764, 24470, 25860, 26350, 29915, 29927, 33207, 34917, 35564, 35890, 39015, 39994, 41069, 42440 (6); 20185, 35412 (7); 2322, 3539, 38948 (6a); 27740, 28711, 28747, 28791, 28861, 28905, 36815 (10); 27779, 27795, 27796, 30009, 36296, 39808, 39833, 40470, 40471, 42391 (9); 31358, 36855, 36859, 36902, 36950, 36967, 37048, 37197, 37343, 37398, 37835, 37858, 38097 (12); 38025, 38037 (18).

Palmer, W.—1340 (1).

Pammel, L. H.—14, 52 (9).

Pammel, L. H., & Blackwood, R. E.—3623, 3876, 3887, 4063 (18).

Pammel, L. H., & Davy, J. B.—77 (17).

Parish, S. B.—453, 1290, 10882, 11969 (18).

Payson, E. B.—248, 982, 1066, 1077, 2307, 4779 (18); 1069, 1075 (12); 1051 (16).

Payson, E. B., & Armstrong, G. M.—3272 (12).

Payson, E. B., & Payson, L.—1812, 2540, 3883, 3884, 4225, 4228 (18); 1812 (12).

Pease, A. S.—678 (6); 670, 10995, 14374, 16044, 26527 (3); 683, 16554, 16990, 17890, 18048, 19680, 23232, 24246, 25775, 25912, 25979, 26323, 26541 (9); 20216 (11); 4090, 10216, 10312, 11205, 11969, 13482, 14372, 16662, 16683, 19561, 25275 (1); 16010, 17476, 18044 (5); 19794 (10); 22360 (12); 24229, 26992 (7).

Pease, A. S., & Bean, R. C.—26215, 26502 (10).

Pease, A. S., & Long, B.—21434, 21452 (9); 21453 (7).

Pease, A. S., & Ogden, E. C.—24884, 25152 (11).

Peck, M. E.—3530, 8512, 8731, 9242 (17).

Peebles, R. H.—13920 (18).

Peebles, R. H., & Parker, H. W.—14670 (18).

Pennell, F. W.—82, 24805 (5); 2708, 12027 (9).

Pennell, F. W., & Long, B.—7559 (5).

Perry, L. M., & Roscoe, M. V.—243 (2); 244 (1).

Phelps, O. P.—567, 1591 (5); 568, 1592 (10); 1581, 1582 (6); 1583, 1584, 1585, 1586 (9); 1588, 1589 (1).

Piper, C. V.—84 (13); 1534 (12); 2694, 3812 (14); 3823 (15).

Piper, R. H.—76881 (9).

Plantae Exsiccatae Grayanae—662 (7); 663, 664 (5); 842 (9); 959 (1).

Porter, C. L.—1059 (18).

Potter, D.—484, 485 (11); 486, 487 (1).

Pretz, H. W.—2363a, 3246, 5919, 9090 (5); 8296, 9260 (8); 10767, 11248, 11762, 12754 (9).

Purpus, C. A.—5376, 6523 (18).

Rand, E. L., & Robinson, B. L.—616 (1); 618 (9).

Randolph, L. F., & Randolph, F.—121 (5); 1200 (6).

Raup, H. M.—2645, 2647, 2648, 2649, 2650, 2652, 2653, 2654, 2656, 6065, 6084, 6588, 6670, 6931, 6933, 7078, 7089 (12); 7410, 7727 (6); 8094 (9).

Raup, H. M., & Abbe, E. C.—3500, 3502, 3530, 4466, 4515, 4519 (12).

Rehder, A.—955 (7); 115, 116 (18).

Ridgway, R.—2534 (6).

Robinson, B. L.—782 (1).

Roland, A. E.—2047, 41469 (9).

Rolland, F.—57, 58, 59 (6); 7214 (3); 13033, 13035 (9).

Rolland-Germain, Fr.—19258 (10).

Rollins, R. C.—198 (18); 550 (12); 840 (14); 889 (16).

Rollins, R. C., Dillon, L. A., & Pickett, F. L.—868 (12).

Rosendahl, C. O.—439, 4935, 4937, 5198 (4); 4980, 4983 (9); 6072 (10).

Rosendahl, C. O., & Brand, C. J.—88 (13).

Rosendahl, C. O., & Butters, F. K.—2578, 3892 (4).

Rosendahl, C. O., & Nielsen, E. L.—1852 (5).

Rossbach, G. B.—1102, 1136 (6).

Rousseau, J.—24557, 24552 (3); 24537, 24550, 24554, 24561, 26241, 26259, 26478, 26513, 26672, 32418 (11); 26228, 26771 (1); 24549, 24559, 24562, 24567 (5).

Rousseau, J., & Fortier, L.—31441 (1).

Ruth, A.—317 (6).

Rydberg, P. A.—680 (12); 9052 (6).

Rydberg, P. A., & Carlton, E. C.—6662 (18).

Rydberg, P. A., & Garrett, O. A.—9274 (18).

St. John, H.—11887 (9); 1903, 90526, 90527, 90528, 90529 (1); 1909 (2).

St. John, H., & Long, B.—1009, 8059 (6); 1063 (7).

St. John, H., & Nichols, G. E.—2332 (1).

Sandberg, J. H.—3 (9).

Sandberg, J. H., & Leiberg, J. B.—94 (12).

Sandberg, J. H., MacDougal, D. T., & Heller, A. A.—26 (12) ; 53 (15).

Sandborger, J. D.—20 (1).

Sanford, J. N.—379 (6).

Sanford, S. N. F.—626 (9) ; 1066, 1193, 10215 (5).

Sargent, H. E.—21 (7) ; 24 (6).

Schacklette, H. T.—261 (6).

Seymour, F. C.—571, 1222, 3493 (7) ; 1223, 1224, 3501 (5) ; 1708, 1709, 3512, 4641 (9).

Shantz, H. L.—345 (12).

Sharp, A. J., & Svenson, H. K.—7278 (6).

Slavin, B. H.—203 (9) ; 205 (10).

Smiley, F. J.—214, 215, 899 (17).

Smith, E. G.—12005 (18).

Smith, L. B., & Hodgdon, A. R.—3872 (6).

Smith, L. E.—284 (17).

Solheim, W. G.—434 (18).

Sonne, C. F.—88 (17).

Spencer, M. F.—865 (17).

Spiegelberg, C. H.—341 (14).

Spreadborough, W.—93904, 93905, 93906, 93907 (13).

Standley, P. C.—4125 (18).

Stanford, E. E.—1758 (17).

Stecker, A.—19 (1).

Stevens, G. W.—2427 (6).

Stevens, O. A., & Graves, H.—278 (11).

Steward, A. N.—230 (13).

Steyermark, J. A.—7009 (10) ; 18635 (9).

Stone, W.—65, 6484 (7) ; 11932 (5) ; 12684 (9).

Stoudt, H. N., & Hermann, F. J.—2779, 2784 (6).

Suksdorf, W. N.—52, 841, 8585, 8597, 8609, 10025, 10026, 10129, 10154, 10234, 10247, 11841, 11859 (12) ; 269 (18) ; 8575 (14) ; 2138, 2139, 2153, 10033, 10154, 10194, 10195, 10201, 10360, 10361, 10382, 10395, 10455, 10494, 11835, 11841, 11859, 11973 (13).

Svenson, H. K.—346, 7779 (6) ; 7849 (10) ; 8012 (9).

Tanger, Louise F. A.—3025 (6) ; 3036, 3044, 3045 (5) ; 3043, 3065 (9) ; 3351 (8).

Thompson, J. W.—6002, 11386 (14) ; 7073 (12) ; 616, 2714 (13).

Thone, F.—172 (6).

Tidestrom, I.—9359, 9429, 9460, 9600, 11050 (18) ; 11882 (6) ; 11947 (7).

Topping, D. L.—223 (5).

Torrey, J.—126 (16).

Tower, A. O., & Seymour, F. C.—3664 (10) ; 3668, 3671 (9) ; 3674 (6).

Ulke, T.—S35 (12).

Visher, S. S.—3308 (12).

Voorhies, C. T.—82 (18).

Wahl, H. A.—29, 298 (5) ; 34 (6) ; 33, 47, 73 (9).

Walker, E. P.—210, 416 (18) ; 1075 (13).

Watson, S.—353 (18).

Weatherby, C. A.—2018, D2103, 3616, 4070, 4070a, 4070b, 4255, 5370 (9) ; D2157 (6) ; 2861, 5280 (5) ; 4916, 7029 (7).

Weatherby, C. A., Smith, L. B., Rollins, R. C., & Muñoz, C., Pl. Exsicc. Gray. —959 (1).

Webb, R. J.—84 (6) ; 1180 (5).

Werner, W. C.—54 (9) ; 55 (6).

Wetmore, A.—470 (18).

Wherry, E. T., & Adams, J. W.—2768 (9) ; 2775 (7).

Whited, K.—363 (14) ; 571 (12) ; 1197 (13).

Wiegand, K. M.—991, 2131, 2132, 2539, 2541, 15627 (7) ; 2133, 4290, 6587, 6593, 6594, 6603 (9) ; 2498, 2499, 2501, 2505, 4281, 6582, 6589, 6592, 13976, 13979 (10) ; 2136, 2572 (5).

Wiegand, K. M., & Eames, A. J.—2515, 2517, 2518 (7).

Wiegand, K. M., & Manning, W. E.— 1328, 1330, 1331 (7).

Wiegand, K. M., & Metcalf, F. P.— 6583 (10).

Wiggins, I. L.—4631 (17).

Wiggins, I. L., & Demaree, D.—4948 (18).

Wilkens, H.—471, 5128, 5168 (9) ; 5129, 6666 (5) ; 1097 (6).

Williams, L. O.—577 (18) ; 1106 (12).

Williams, L. O., & Williams, R.—3305 (12).

Wislizenus, F.—937 (10).

Wolden, B. O.—1043, 1047, 1074, 1075, 1078 (9) ; 1353 (10).

Wolf, C. B.—2988 (18) ; 3075 (12).

Woodward, R. W., & Bean, R. C.— 17116 (7).

Woodward, R. W., & Fernald, M. L.— 15202 (9).

Zech, O. F.—152, 161, 168, 195 (4).

Zeller, S. M., & Zeller, E. B.—844 (13).

PLATES
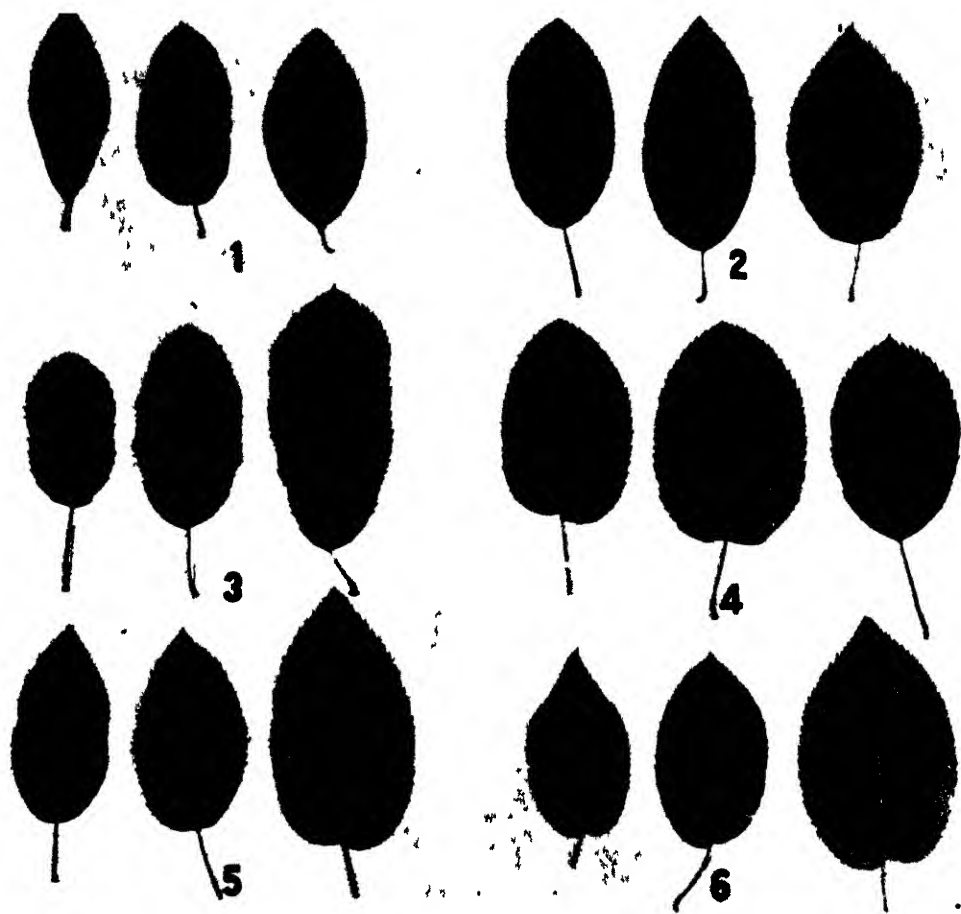
PLATE I

Leaves of species of *Amelanchier* from herbarium specimens

Fig 1—*Amelanchier bartramiana* (Tausch) M Roem

Fig 2—*Amelanchier neglecta* Egglest

Fig 3—*Amelanchier fernaldii* Wieg

Fig 4—*Amelanchier interior* Nielsen

Fig 5—*Amelanchier laevis* Wieg

Fig 6—*Amelanchier arborea* (Michx f) Fernald

102
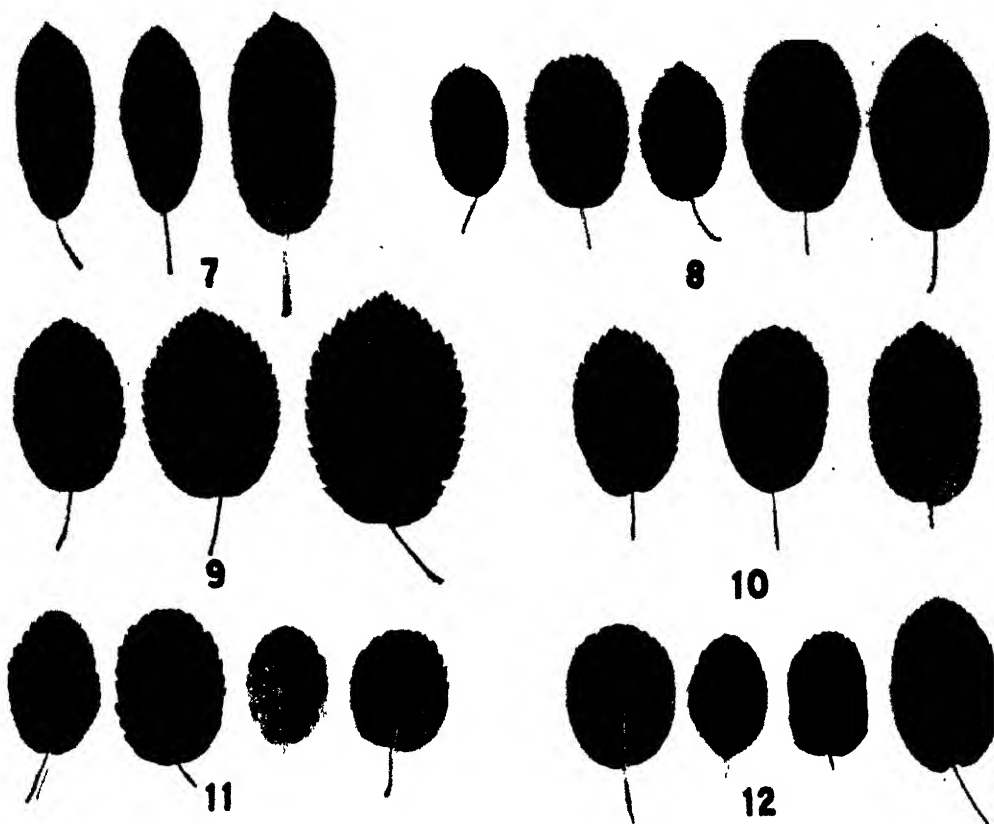
PLATE II

Leaves of species of *Amelanchier* from herbarium specimens.

FIG. 7.—*Amelanchier canadensis* (L.) Medic.
FIG. 8.—*Amelanchier spicata* (Lam.) K.Koch.
FIG. 9.—*Amelanchier sanguinea* (Pursh) DC.

FIG. 10.—*Amelanchier gaspensis* (Wieg.)
    Fernald & Weatherby.
FIG. 11.—*Amelanchier alnifolia* Nutt.
FIG. 12.—*Amelanchier florida* Lindl.
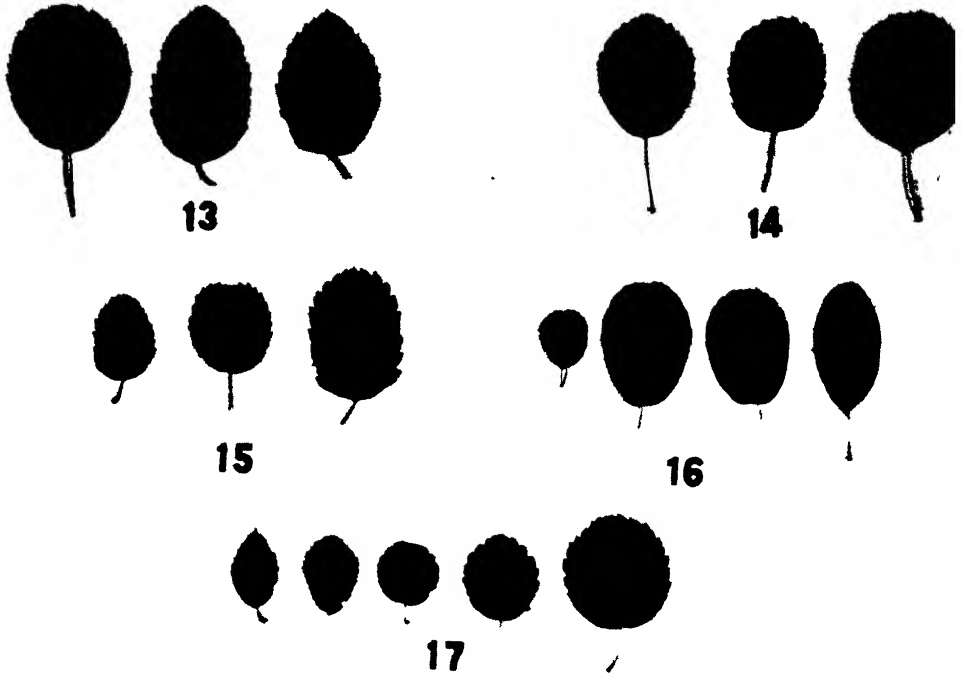
PLATE III

Leaves of species of *Amelanchier* from herbarium specimens.

Fig. 13.—*Amelanchier cusickii* Fernald.   Fig. 16.—*Amelanchier pallida* Greene.
Fig. 14.—*Amelanchier basalticola* Piper.   Fig. 17.—*Amelanchier utahensis* Koehne
Fig. 15.—*Amelanchier pumila* Nutt.

PLATE IV

Type of *Amelanchier fernaldii* Wieg. in the Gray Herbarium; from Fernald, Long & St. John 7592, Grindstone Island, Magdalen Islands, Quebec, Canada.

PLATE V

Type of *Amelanchier neglecta* Egglest in the Gray Herbarium, from
Rutland, Vermont, May 12 and June 21, 1899, W W Eggleston

PLATE VI

Type of *Amelanchier laevis* Wieg. in the Gray Herbarium; from Wellesley, Massachusetts, K. M. Wiegand 2136.

PLATE VII

Type of *Amelanchier interior* Nielsen in the Herbarium of the University of Minnesota; from Minneapolis, Minnesota, E L Nielsen 2961

Fig. 2

Fig. 1

PLATE VIII

FIG. 1.—Phototype from Herb. Mus. Paris of F. A. Michaux's *Mespilus canadensis* var. β *cordata*, the basis of *Amelanchier arborea* (Michx.f.) Fernald.

FIG. 2.—Phototype from Herb. Mus. Paris of Michaux's *Mespilus canadensis* var. α *obovalis*, the basis of *Amelanchier obovalis* (Michx.) Ashe.

109

Fig. 1

Fig. 2

PLATE IX

Fig. 1.—Phototype of *Mespilus canadensis* L. (*Amelanchier canadensis* (L.) Medic.), from the Linnean Herbarium, London. Reproduced from Rhodora, vol. 43, pl. 672, fig. 1.

Fig 2.—Type of *Amelanchier pumila* Nutt., from the specimen in the herbarium of the Academy of Natural Sciences, Philadelphia.

PLATE X

Photograph of *Amelanchier intermedia* Spach in the Gray Herbarium.
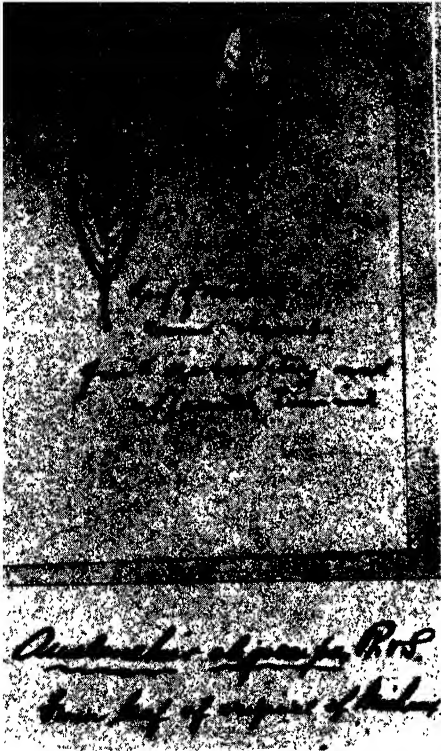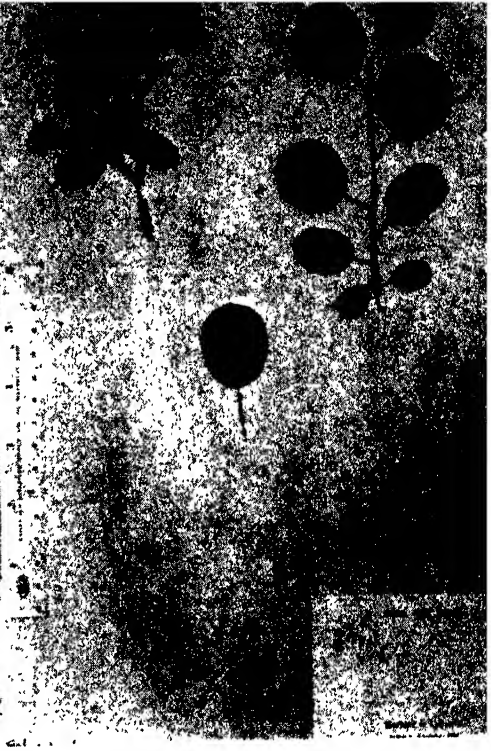
Fig. 1   Fig. 2

PLATE XI

FIG. 1.—Photograph of a tracing of leaves of *Mespilus canadensis* var. δ *oligocarpa* Michx. from Herb. Mus. Paris. This is *Amelanchier bartramiana* (Tausch) M.Roem.

FIG. 2.—Phototype of *Crataegus spicata* Lam. in Herb. Mus. Paris, the basis of *Amelanchier spicata* (Lam.) K.Koch.

PLATE XII

Type of *Amelanchier stolonifera* Wieg. (Gray Herbarium).

PLATE XIII

Photograph of the second sheet of *Amelanchier stolonifera* Wieg
(Gray Herbarium)

PLATE XIV

Photograph of the third sheet of *Amelanchier stolonifera* Wieg.
(Gray Herbarium).

115

PLATE XV

Type of *Amelanchier humilis* Wieg in the Gray Herbarium

PLATE XVI

Photograph of an isotype of *Amelanchier austromontana* Ashe
in the Gray Herbarium

117
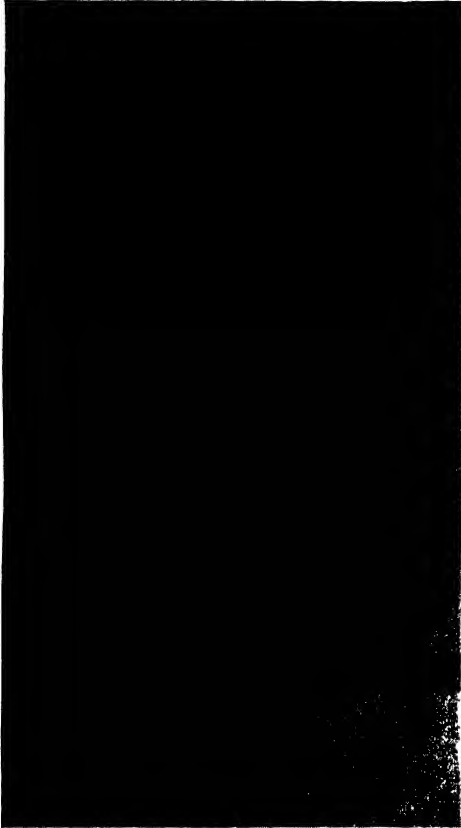
Fig 1   Fig 2

PLATE XVII

FIG. 1.—Phototype of Michaux's *Mespilus canadensis* var. γ *rotundifolia* in Herb. Mus. Paris
FIG. 2.—A tracing of part of specimen shown in Fig. 1, from the original in the Gray Herbarium.

PLATE XVIlI

Photograph of a specimen of *Amelanchier sanguinea* (Pursh) DC. from Minnesota.

PLATE XIX

Type of *Amelanchier gaspensis* (Wieg) Fernald & Weatherby
in the Gray Herbarium.

PLATE XX

Type of *Amelanchier cusickii* Fernald in the Gray Herbarium.

UNIVERSITY OF ILLINOIS

Amelanchier pallida Greene

G. N. JONES 1942

FLORA OF N. CALIFORNIA.

PLATE XXI

Photograph of an isotype of *Amelanchier pallida*

PLATE XXII

A flowering specimen of *Amclanchier obovalis* (Michx.) Ashe in the herbarium
of the Academy of Natural Sciences of Philadelphia, collected
in Virginia by Fernald & Long, no. 7073.

PLATE XXIII

A fruiting specimen of *Amelanchier obovalis* (Michx.) Ashe in the herbarium
of the Academy of Natural Sciences of Philadelphia, collected
in Virginia by Fernald & Long, no. 9947.

INDEX TO PLANT NAMES

MINIMUM AREAS FOR

DIFFERENT VEGETATIONS

Their Determination from Species-Area Curves

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CONTENTS

INTRODUCTION

MANY STUDIES in ecology, agronomy, forestry, and range management have been made upon sizes, numbers, and arrangements of plots and study-areas of vegetation. Interest has commonly centered upon ecological or statistical method, or even more frequently upon economy of sampling. In this paper, emphasis is chiefly upon extent and the concomitant variation in number of species both as a phenomenon of vegetation and as an important characteristic by which different communities or different stands may be compared. A simple and widely applicable means of making such comparisons is offered, with results of applying it to about 240 examples of vegetation in many parts of the world. Briefly, the method is to use data for different-sized areas in a community to construct an S-shaped species-area curve on semi-logarithmic paper. The second step is to locate upon this curve two "reference areas," by means of conventionally adopted ratios of one to the other, as to both extent and number of species. A particular reference area of one vegetation is considered to be equivalent, in at least certain respects, to the same reference area of any other vegetation.

The writer is indebted, for use of data and for other cooperation, to officers of the California Forest and Range Experiment Station, particularly to Jerome S. Horton of its Glendora office; and for mathematical guidance to Dr. Paul B. Johnson of Occidental College, for a time at the Glendora office. During later stages, Dr. E. L. Welker, University of Illinois, more recently statistician for the American Medical Association, was mathematical adviser. Dr. John E. Potzger, Butler University, has furnished detailed plot data for numerous forests. The figures were drawn by Professor John E. Pearson, University of Illinois. The writer is very grateful for these substantial aids.

DEVELOPMENT OF THE METHOD

The curves first used were drawn to linear co-ordinates; later, number of species was plotted against logarithm of area. Semi-logarithmic paper is convenient for this purpose. After a number of trials, the hypothesis at first followed, that species-number varies directly with log of area, and that the curve consequently should be a straight line, was found to be untenable. All communities necessarily yield a curve which is concave in its lower or small-area section. Communities with data for sufficiently large areas, so far as studied, show a convex upper section, indicating a decline in species-increment from the logarithmic rate. Facts which presumably account for this decline will be given later. The curve thus has an S-form.

The difficult problem with a species-area curve has been to locate upon it one or more definite and strategic points or stopping-places which can be identified with certainty. If an area can thus be identified, it can serve as an effective plot-size, or as a larger study-area which will surely include all important species and a sufficient number of the less common species, including those especially characteristic of the type. The several proposals thus far made toward this problem have proved illusory. They give different results if the scale of one of the two variables is altered, or if they depend upon an accidentally determined largest area studied in the field. The problem is perhaps insoluble, but practical utilization of species-area curves to determine what are called reference areas is not difficult. A reference area is one yielding a definable degree of information concerning the stand or type in which it lies. It can be determined by several means of intensive study within a particular vegetation. Connections between numbers of species and degrees of informativeness have been found for several sizes of reference area in a study of trees in two old-growth mixed forests in Illinois by Vestal and Heermans (1945). They learned (p. 129) that the plot-size with half as many species as in a fair-sized stand was the same as that which qualified as the "smallest representative area," and that (p. 130) an area five times the small one, "large enough to include all important species and nearly half of the minor species, should be large enough to show many characteristics of the type." This intermediate area clearly identifies the type of forest; it provides a minimum statement of composition with approximate ranking of species as to number of trees and as to some measure of bulk or of ground-space occupied. It is called "minimum area for assignment to type," or briefly "minimum area." It is too small to give a dependable picture of diameter-distribution (form of stand). The "fair-sized stand" mentioned, a third reference area, is 50 $\times$ the smallest representative area, 10 $\times$ the minimum area.

If these different-sized pieces of one vegetation show definite ratios of species-number with particular area ratios, is it likely that similar relations will hold for other vegetations? The question seemed to deserve a test. Given certain field

2

data, it should be possible to determine actual values of reference areas for almost any vegetation, since their relative values are defined in terms of one another; i. e., the smallest representative area is that size which, having one-fiftieth the extent of another, includes half as many species. As a concrete example, we may ask whether the 136 milacres identified as the smallest representative area for a pine forest in Wisconsin is equivalent (i.e., comparable in many respects) to the 803 milacres found in the deciduous Brownfield Woods in Illinois. There are strong indications that they are equivalent. For this pine forest and for many other communities studied it is evident that all of the principal species are included in the smallest reference area. More detailed evidence is not yet sufficient to tell how close the equivalence may be. It can be said after trials with many kinds of vegetation that the results appear to be consistent with one another, and with the described characteristics of the different kinds of plant cover treated.

Restating the hypothesis: It is proposed that reference areas be defined in terms of ratios of area and of number of species, the conventional ratios adopted being those found after intensive study in one particular forest; and that reference areas so identified for different kinds of vegetation are presumably equivalent to one another in many respects, chiefly as to degree of informativeness.

While on a species-area curve no one strategic point can be singled out, any two points related to each other by predetermined ratios such as 1 : 50 for area and 1 : 2 for species-number, can be fixed upon with certainty. This possibility occurred to the author during the summer of 1944 while studying species and area in chaparral communities, and while the graphs were being drawn as sloping straight lines. The problem was submitted for mathematical scrutiny to Mr. Paul B. Johnson, statistician, then at Glendora, California.

He quickly proved that the two points were readily determinable, and resolved the problem into a simple case of two linear equations with two unknowns, having a unique solution. Fig. 1 illustrates the problem of locating two reference areas, Ar and Af, on a straight-line graph. Numbers of species at these areas are respectively Sr and Sf. (The "r" signifies smallest representative area, "f" is for fair-sized stand.)

The sloping line, drawn through points representing particular species numbers at particular areas, is the species-area graph. Locations of Ar and Af are to be determined. Two constants incidental to the problem are a, number of species at unit area, and b, the slope or pitch of the graph. Mr. Johnson has kindly furnished the following compact algebraic statement. It is in general terms, applicable to any species-number and area ratios which might be adopted, with the addition (in brackets) of quantities dependent on the particular ratios here used:

$$\text{The significant ratios are:} \frac{Af}{Ar} = r \ [= 50],$$
$$\text{and,} \frac{Sf}{Sr} = v \ [= 2].$$

The required values are: $Sr = \dfrac{b \log r}{v - 1} \left[= \dfrac{b \log 50}{1} \right]$.

$$Ar = \text{antilog } \frac{Sr - a}{b}.$$

$$Sf = v \, Sr \, [= 2 \, Sr].$$

$$Af = r \, Ar \, [= 50 \, Ar].$$
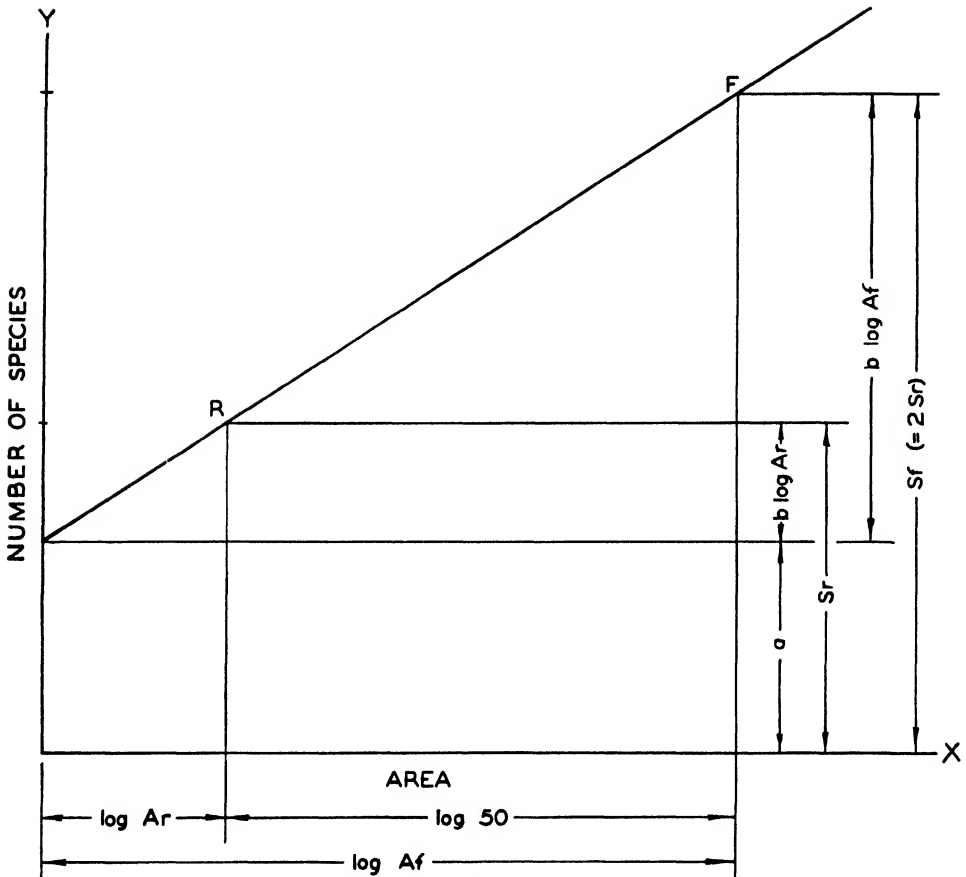
FIGURE 1. The problem of locating two areas, Ar and Af, with predetermined species-number and size ratios on a species-area graph assumed to be a straight line. See text.

A trial-and-error method of locating Ar and Af is simpler and quicker than the algebraic solution, and unlike the latter, can be used on S-curves. One puts on a slip of paper two marks separated by an interval representing a fifty-fold increase of area on the logarithmic scale used. First one judges visually the approximate levels for the two points, the upper being twice as high above zero species as the lower. Then, with the left-hand mark on the curve at the presumed lower point, or "trial Ar," one reads species-numbers for the two points. If the species-number read at the presumed Af is less than twice the other, the trial areas are larger than need be; if more than twice, smaller. Shifting in the proper direction, one writes down species-numbers for one pair of areas slightly up-slope, and for another pair slightly down-slope, of the true but still unknown positions. Then the exact values are found by interpolation. In the following

example, C is the computed Sf, $= 2 \times S$ at trial Ar; G is the species-number read from the graph at the presumed Af; and d's are differences.

It will be recalled that a reference area of intermediate size, minimum area or

Computation from S-curve
for Kenoyer's *Chamaedaphne* bog near Kalamazoo

	Trial Ar *milacres*	S at Ar	Af, $= 50$ Ar *milacres*	C	G	C — G
	2.2	15.30	110	30.60	30.36	+0.24
	2.1	15.10	105	30.20	30.23	—0.03
d's	.10	.20	5.0	.40	.13	.27
d's $\times$ ³⁄₂₇	.011	.022	0.555	.044	.014	
	2.11	15.12	105.55	30.24	30.24	
	Ar	Sr	Af	Sf		

Am, has been mentioned. It is perhaps more significant than either Ar or Af. It is found, after the other two are known, from its conventionally defined area ratio, $5 \times$ Ar. It occurs, in all instances thus far determined, on the convex part of the curve. Since degree of convexity and beginning place of convexity vary for different communities, the corresponding species number, Sm, is best read from the curve at Am. The ratio of Sm to Sr, if the straight-line logarithmic
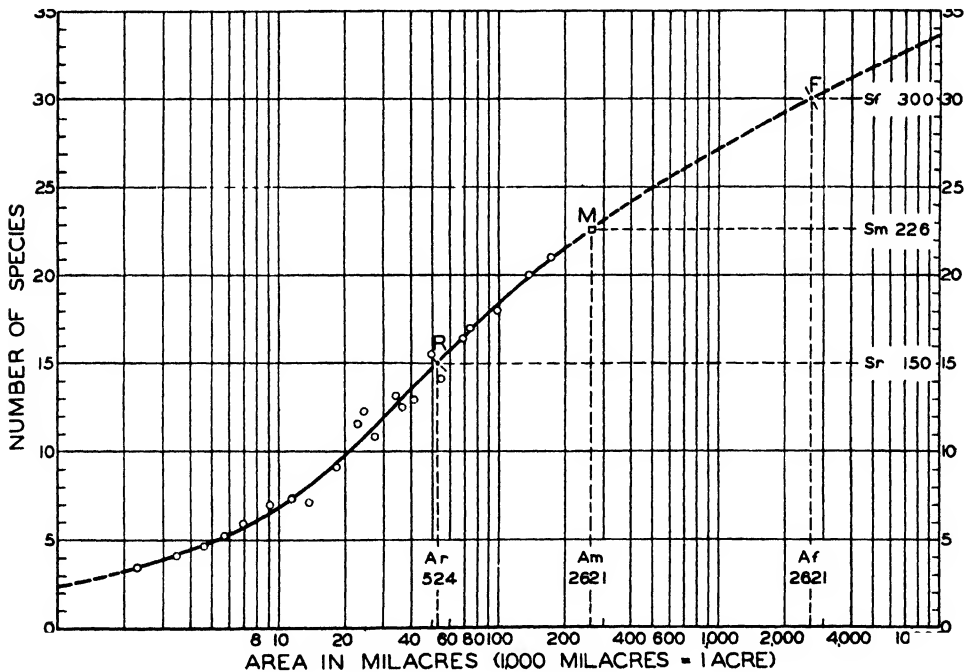
FIGURE 2. A species-area curve of the S-form found to be usual. Oak chaparral at Tanbark Erosion Plots, San Gabriel Range. Data from California Forest and Range Experiment Station. Four leading species. Plot-area basis is 173 milacres, with 21 species. Reference areas are large, since four shrubs, especially *Quercus dumosa* and *Ceanothus crassifolius*, dominate so strongly that little room is left for other species. The marked reference points R, M, and F, identify Ar (smallest representative area) at 52.4 milacres, with 15 species; Am (minimum area) at 262 milacres (1060 sq. m.), with 22.6 species; and Af (fair-sized stand) at 2621 milacres, with 30 species.

graph were the true form for species-area curves, would be a constant, 1.4114. On S-curves it is greater than this, usually between 1.44 and 1.5. In fig. 2 the three reference points are marked upon the curve.

If Sm : Sr were a constant ratio, it would be simpler to locate the two smaller reference areas on the curve, ignoring Af. Because of variations in the form of the curve, because a greater degree of accuracy is attainable with the greater spread of area, and because of a complication which may in a few cases be encountered, it has seemed greatly preferable to use Ar and Af as the areas to be first determined.

The complication, first pointed out by Mr. Johnson, is that on an S-curve there may be *two* pairs of areas which will satisfy both the area and the species-number ratios. One pair is very much smaller than the other, and is located on the concave lower section of the curve. Most sets of species-area data do not include such small areas, and the small pair of spurious reference areas consequently does not appear on most curves.

If they are encountered, there should be no difficulty in recognizing them from their position on a concavity, and from their usually obviously inadequate degree of inclusiveness. There are a few instances in the literature, of species-area data from which extremely small minimum areas were inferred. The curves were plotted to linear coordinates from a very small range of plot sizes, and did give the appearance of adequacy to the less-meager sizes studied. If the curve is drawn with logarithmic area scale, over a sufficient range of sizes, this kind of inference will not be made. The false reference areas will appear less frequently, and will be farther from the real reference areas if the two sizes adopted are separated by a 50-fold area-spread rather than by a 5-fold spread.

Certain floristically-poor communities have at first appeared to give S-curves which fail to include on any part of them a two-fold species increment in a 50-fold increase of area. Those thus far met with do not afford adequate species-area data to demonstrate that this is real; yet it may be so. If so, some other standard must be adopted for such communities, such as the use of an Sf : Sr ratio smaller than 2, say 1.7, or use of Am : Ar and Sm : Sr ratios only. The rather scanty data for the floristically-poor communities studied lend themselves to construction of curves which do give a 2-fold increment.

Mr. Johnson has suggested that if or when a sufficient degree of dependability and precision in the obtaining of field data and construction of S-curves permits a better understanding of their properties, it may be possible to recognize a strategic point from the form of the curve itself. He looks for such potential significance to the point of inflection (or "flex point"), at which the change from concavity to convexity takes place. At present the curves cannot be drawn with sufficient degree of certainty to know just where the flex point should be. The geometric determination of a significant area is thus not yet feasible. Yet it may be noted that the small reference area, Ar, is usually near, or not far above, the flex point (see Fig. 2).

CONVERSION OF DATA TO SERVE
AS BASIS FOR CURVES

(Readers interested only in results may omit this section.)

Since regrettably few sets of plot data are published in full, and since the methods and objects of obtaining them vary so greatly, it was necessary to modify much that is usable in published or otherwise accessible material, adapting it to the present end of constructing species-area curves. For this reason many curves made for this study are from too scanty or uncertain figures, and reservations are stated along with the results. Much that is available and of great promise has had to be left unworked.

FROM NOMINAL TO EFFECTIVE PLOT-SIZE

The practise of Raunkiaer (1909-10) and of some users of his method (Vahl, 1913, Ramaley, 1942) has been to count as included within the small plot-size of 0.1 square meter all plants whose crowns extend over any part of the plot. Effective plot-size is thus greater than stated area, and is greater for plants with larger crown-spread. Raunkiaer plots are usually arranged along one straight line, and are well separated at uniform interval in any one set of 50 .1-sq.-m. plots. Such plots are difficult to compare with contiguous plots, usually larger, in which rooted shoots must usually be present to be counted. Contiguous plots are more amenable to species-area study. For each set of separated small plots of the Raunkiaer type an independent judgment must be made to estimate a likely plot size. Usual estimates are 2 to 4 $\times$ nominal plot size. In an extreme case, Ramaley's sagebrush in the San Luis Valley of southern Colorado (1942: Table 8), his additional statements of plant-size and open spacing enable one to infer that the 210 bushes recorded in his 200 0.1-sq.-m. plots are as many as would normally be found in 61.8 milacres. The effective plot size is estimated to be 0.309 milacres or 1.25 sq. m.; 12.5 times the nominal plot area.

Du Rietz has also followed Raunkiaer's convention of including plants which overlap from outside; he has used many plot-sizes; for his *Pinus–Calluna* at Sandön (1921:153), 0.01 to 16 sq. m. For this the conversions used are: nominal .01 sq. m. to effective .03 milacre; .04 sq. m. to .06 mlc.; .25 sq. m. to .2 mlc.; 1 sq. m. to .3 mlc.*

FROM SEPARATED PLOTS TO ONE-PIECE EQUIVALENT AREA

A distinction is made between a sizable unit of vegetation in one piece and of compact shape, and the more commonly studied group of separated plots or

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* "Mlc." is used as a coined abbreviation for milacre: the unit of area found generally convenient. It equals 43.56 sq. ft. Milacre plots, 6.6 feet on a side, are commonly used by American foresters for tree seedlings. Such a plot is a little over 4 square meters (4.04687). Multiplying number of milacres by 4 gives fair approximation to metric areas. One square meter equals 0.2471046 milacres. In the section giving results from curves, minimum areas are stated in square meters as well as in milacres.

strips having the same aggregate area. Not all characteristics of the one-piece unit are the same as those of the aggregate. The latter is generally used because it provides a larger assortment of species and a more inclusive sample of the always-present variations in both site conditions and plant cover. In this understandable striving for economy, certain features and individualities of the one-piece areas in sizes larger than the usual plots may have been overlooked. Since a point on a species-area curve represents an integral area, estimates converted from plot-aggregates are required. This is one of the greatest difficulties encountered. Fortunately a standard was at hand for aid in estimating equivalents for groups of 100-sq.-m. tree plots, many of which were contributed by Potzger and Friesner and their associates, notably Scott McCoy. This standard is a grid of 64 contiguous tenth-acre tree plots, completely mapped, from Trelease Woods near Urbana, Ill., one of the two forests studied intensively. The one-piece areas required were to be equivalent to alternate-plot strips of varying length (plots enumerated alternating with blank areas of equal size). From the grid were selected strips of alternate plots of fortieth-acre size (just larger than 100-sq.-m. plots). Their species-numbers were counted for varying lengths of strip, one-piece areas giving these numbers of species were found from the species-area curve for the grid, and results were put together in a simple graph. From this graph, multipliers were found which give approximate one-piece equivalents for a considerable variety of separated-plot combinations. Thus:

Equivalents for Alternate-Plot Strips of 25-Milacre Tree Plots							
No. of plots in strips	5	10	15	20	25	40	50
Equivalent one-piece area (in plot units)	5.5	12.2	20.2	29.6	40	68	86.5
Multiplier	1.1	1.22	1.35	1.48	1.6	1.7	1.73

The larger a plot-size (considering also the size of plants in the vegetation studied) the smaller is the multiplier to be used. The more remotely plots are separated, the larger the multiplier. One long line of plots samples a larger area than the same number of plots (with the same interval between plots), arranged in several parallel lines. From such considerations judgments were made of one-piece areas equivalent to the various groupings of plots in the data available from many sources. The total area equivalent to a grouping of 50 small plots in one long line (the Raunkiaer plan) was taken to be 1.73 × 50 × the effective plot-size used.

FROM F% OR FREQUENCE OF OCCURRENCE IN PLOTS, TO AVERAGE NUMBER OF SPECIES PER PLOT

Many enumerations of plot-aggregates fail to give details for individual plots, or to state the average number of species per plot. If, however, the statement includes number or percentage of plots in which each species occurs, and if the species are completely listed, it is simple to compute species per plot. In a sense, frequence and species-per-plot bear inverse relation to each other. One tells

about species in terms of plots, the other about plots in terms of species. To find species-per-plot, consider each occurrence of one or more individuals of one species in one plot to constitute one "occurrence." The total of occurrences for one species is the number of plots in which it occurs. Add the occurrences for all the species to get total of occurrences. (This total appears as the number of "points" in many of Raunkiaer's columns for particular lines of 50 plots.) Divide total occurrences by number of plots in the aggregate. The quotient is the average number of occurrences per plot, which is the same as average number of species per plot. If proof is needed, try it on any known set of data.

It makes no difference whether plots are scattered or contiguous: the quotient is the correct average species-number for the plot-size or the effective plot-size.

While a series of species-numbers from which a curve is made is expected to come from a single stand, yet it may in certain instances be permitted to combine data from different stands not too unlike and within the same district. This makes possible a use of data such as those of Du Rietz, Fries, Osvald, and Teng-wall (1920), and of Du Rietz (1921) for vegetation in northern Europe. In such cases, if no statement is given of species-per-plot, the given constance percentages can be used to determine average number of occurrences per plot in exactly the manner described for frequency. If the curve is a composite from different stands, that fact should be specified.

FROM LARGER OR SMALLER TREE-DIAMETER-LIMIT TO THREE-INCH LIMIT

It is not possible to compare different forests if the lower limit of size of trees included is appreciably different. For different reasons the limit actually used varies widely. Conversion to the same limit is much easier if given data include trees smaller than the limit adopted, since it is safer to exclude than to extrapolate. The limit here used is three inches (7.72 cm.) at breast height. This is not greatly different from either the 7-cm. or the 10-cm. limit commonly used.

Various expedients have been used to convert number of trees per acre from one limit to another. Some of the Philippine forest examples (and others in the tropics) enumerate small trees in small plots by height-classes, and larger trees in larger plots by diameter-classes. A few tables listing trees in the same plots by both types of size-class permitted the making of simple graphs roughly correlating numbers by height with numbers by diameter. These are of limited applicability but in certain cases made enumerations usable.

Most conversions from one limit to another were done by constructing a stand curve or cumulative stand curve for the particular forest. The latter type was made from a table in which the total number of trees in an area was stated for successively larger limits, as 3 inches diameter and larger, 6 inches and larger, 9"+, 12"+, to whatever largest limit is appropriate. Each such total makes one point on the cumulative stand curve. The most useful of these curves was

one modified from a normal stand curve for old-growth deciduous forest made by the author and Audrey H. Benedict (see Benedict, 1945). From it could be found a "likely proportion" for converting from one limit to another. It seems to apply much more generally than to merely its own type of forest. Thus if an acre contains 92 trees of 8-inch diameter and larger, how many trees 3" and larger are likely? On the graph, one reads 77.2 trees at 8" and 151.74 at 3". The likely number sought is 151.74 / 77.2 × 92, = 181.

If it was feasible to convert by each of several methods, this was done, and the results checked one against the other.

CHANGE OF SPECIES-NUMBER FOR CHANGED NUMBER OF INDIVIDUALS

Each conversion in number of trees involves a change in number of species, making a more difficult problem to solve. Two principal approaches may be used. The cumulative table from source materials lists not only trees at each of several diameter limits, but also numbers of species at the same limit. A graphic extrapolation or interpolation is usually satisfactory. This can be checked by another means. Graphs were arbitrarily constructed on semilogarithmic paper, plotting number of species against logarithm of number of individuals, in a family of concave curves patterned after those for Fisher's series in the publications by Fisher, Corbet, and Williams (1943), and Williams (1944). The arbitrary construction similarly spaces the curves evenly between an upper limiting logarithmic curve in which each individual represents a different species (maximum richness of composition), and a lower horizontal limit representing a single species for all possible individuals. In using such graphs a known combination of tree-number and species-number locates a point on or near a particular one of the set of curves. Following this curve right or left to the converted tree-number brings one up or down to the level representing its approximate number of species. Such an approximation is safer when the curve is followed left and down, and when the distance followed is small.

ANALYSIS OF PLOT-MAPS, AND RANDOM SPOTTING

If a description of vegetation includes a map of a large plot or more sizable area, showing individual plants identified by species, it is a simple process to subdivide it to derive figures for smaller plot-sizes. In this process, transparent or translucent overlays marked off into rectangles of appropriate area are convenient, permitting one to utilize the whole area for almost any plot-size chosen. It is sometimes feasible to use a rectangle with length equal to 1.414 times the width. Half-plots and quarter-plots thus have the same proportions as whole plots. Whatever the size, all units have the same shape, thus eliminating any possible fluctuations from this factor. It has been found that there is no significant difference due to shape of plot if length is no greater than twice the width.

If descriptions do not include maps, but give numbers of individuals for the different species in a stated area, a plot-map can be simulated by random spotting. It is a less laborious process if number of species is small. The one-to-several very abundant species can be omitted from all plot sizes which are certain to include one or more individuals of each. From analysis of considerable areas of forest it has been found that the size large enough to contain an average of 3 individuals is likely, in a simple community of few species, to include the species in 97 to 100% of the plots. In a moderately-mixed community with 20 to 35 species, the two or three more abundant species are likely to be less evenly distributed, and require a plot-size containing 6 individuals on the average, to give 97 to 100% frequency of occurrence.

The chance determination of a particular spot to represent the location of a plant was by means of a wide ring of heavy sheet brass. It was made to oscillate on the map, at the same time rotating slowly. When it came to rest, a mark on its outer edge determined the location of the plant.

In chance distributions of this kind, one is likely to be impressed by the fact that plants (of all species, or of any one more abundant species) are more evenly dispersed over the ground than would result from truly random location. Romell once remarked (1930: 592): "In almost any closed forest association, . . . there seems to be a tendency, easily explained by competition, for the trees composing the main stand to be equally spaced." Thus one finds it necessary, after locating about two-thirds of the required number of spots for the most abundant species, to omit further additions where spots are already clustered rather thickly, and to supply a few spots in the larger blank spaces. (The *exact* locations are in all cases the result of chance.) Thus an approach to the usual degree of evenness of distribution is attained. The opposite type of departure from random dispersal, due to aggregation, is much more frequently pointed out, but the common tendency for most species is toward fairly even spacing.

One application of this method, to forests of few species, was patterned on enumerations by E. A. Ziegler (1904) of blackjack oak (*Q. marilandica* Muench) and black oak (*Q. velutina*), in dunes of the Illinois River. For blackjack, Ziegler listed on 2 acres 295 oaks and 80 hickories (*Carya cordiformis*). Since 4 or 5 other species occur in this type, a hypothetical 16-acre sample was assumed to comprise 4 tree species, with 2858 trees 3 inches d.b.h. (diameter breast high) and over, of which only 10 belonged to the 2 uncommon species. From maps made by random spotting, then subdivided, species-numbers were found for 8 sizes of plots.

Ziegler's black-oak sample covered only 1 acre, with 93 trees in 4 species. Four other species are known to occur in the type, and possibly another 3. A map was made for an assumed 9 acres with 837 trees in 6 species. The species-area curve resulting from its analysis indicates a minimum area of 1144 milacres, only a little larger than Ziegler's sample. It has 4.34 species.

Ramaley's account of *Sarcobatus–Chrysothamnus* bush in the San Luis

Valley of southern Colorado (1942: 264), described 8 plots, each 40 × 80 feet, in a large stand on a salt flat 4 miles southwest of Mosca. The numbers of bushes he gave were spotted into rectangles of given proportions. Plots of about 147 milacres and larger plots (up to 734 milacres and presumably much larger areas) all have the same number of species, 4. The curve was drawn on the assumption that these 4 species are the only bushes within the district which can endure this extreme habitat. Consequently, the curve flattens abruptly into a horizontal line at 4 species, reaching that level at a little over one-eighth acre. The same dominants in less extreme habitats were accompanied by other species, bringing the total to about 10 bush species as shown in Ramaley's Table 2 (p. 245). From lists he made for 1000 0.1-sq.-m. plots in 20 locations, a quite different species-area curve results. This is of the usual form, and gives a minimum area of 46 milacres, with 3.8 bush species. The species-number climbs to 6.5 at 10 acres—still not a highly mixed bush assemblage.

RELATION OF FISHER'S SERIES
TO SPECIES-AREA PROBLEMS

The important contributions of Fisher, Corbet, and Williams (1943), and of Williams (1944), illuminating relationship between numbers of individuals and numbers of species, and applying even more generally to many types of "hollow-curve" phenomena, will undoubtedly be of great usefulness in species-area problems. These two papers were not known to the author until December, 1945. Arbitrary species-individuals curves like those of the Fisher's series were thereafter the chief means of finding a species-number after converting from one tree-size-limit to another, in the manner already described.

It seemed that the Fisher's series and its quantity a, the index of diversity, should also become a principal means of amplifying incomplete data, providing additional points for a species-area curve. There is as yet no assurance that this is a dependable method, since it involves the assumption that the concave part of a species-area curve is practically identical with some one curve of the Fisher's-series form. A test of this assumption will be shown shortly.

It is obvious that a species-area curve as a whole cannot be replaced by a curve of the Fisher's series, since in the latter the steeper upper part of the slope is indefinitely continued at about the logarithmic rate. From a concave lower part it gradually becomes almost straight. A species-area curve for vegetation is clearly affected by added circumstances tending to retard the rate of species-increment, and thereby making its upper section convex.

Another question (with no present answer) is whether the species-individuals relation can help to solve species-area problems in vegetation for which no enumeration of individuals is at hand. (In some grasslands and certain shrubberies it is impracticable to distinguish or even to define plant individuals of certain species. Williams (1944) has essayed to apply the Fisher's series (without access to counts of individual plants) to Gleason's data for ground-cover in deciduous forest and in open parts of aspen woodlands in Michigan (1922, 1925), and to Beumée's ground vegetation in Tectona forests in Java (1922), as briefly tabulated by Arrhenius (1923). S-curves for these same vegetation-units were made for the present article.

A test of degree of correspondence between species-area S-curves and species-individuals curves having constant values of a throughout (called a-curves for brevity) has been applied to particular stands. These are in forest and shrub vegetations. Each enumeration covers a wide range of observed plot-sizes having dependable counts of individuals and species. A uniform ratio for successive plot-sizes was chosen for this test: half of a logarithmic cycle, each area being 3.162 times the preceding one. See Table 1. For each such area (A), the following quantities were noted: number of species (S), as read from the species-area curve; number of individual trees (3″ d.b.h. or over),

or bushes, or shrubs (N); and the index of diversity (a), found from S and N on a large-scale graph based on the table by Williams (1943:53). The values of a are likely to be in error by amounts up to 0.1 unit. For the first forest S, N, and a are given at each area; for other communities only the value of a.

TABLE 1. Values of a at Different areas for Six Communities.*

Area, *milacres*, $= A$		3.16	10.0	31.6	100	316	1000	3162	10000	31623	100000
Brownfield Woods	N		1.25	3.96	12.5	39.6	125.3	396	1253	3960	12527
	S			2.47	5.17	9.09	13.37	17.46	21.20	24.49	27.10
	a			3.0?	3.37	3.65	*3.80*	3.77	3.65	3.54	3.23
Reavis Woods	a		5.15?	*5.25*	4.94	4.92	4.85	4.56	4.28	4.07	3.82
Chamise chaparral	a		1.86	1.73	2.18	2.27	*2.87*	*2.87*	2.78			
Chamise–sage	a		2.80	2.85	*3.83*	3.41	3.38	3.30?			
California bush	a	1.58	1.50	1.50	1.58	*1.63*	1.62	1.58	1.50		
Philippia heath	a	3.25	3.82	4.30	4.62	*4.86*	4.73	4.42			

*For Brownfield Woods at 316 230 milacres, $N = 39\,600$, $S = 29.14$, and $a = 3.08$. Data for Reavis Woods in Morgan County, Indiana, are from Potzger & Friesner (1940). The chamise chaparral stand is in the San Rafael Hills in southern California; the chamise-sage chaparral is on basal slope of Mt. Lowe: the bush is on a nearby alluvial fan. The *Philippia* heath in Mauritius was described by Vaughan & Wiehe (1941).— Note that values of a are far from constant. There seems to be little regularity among the several communities as to the area at which a reaches its maximum (shown in table by italic figures).

This table was supplemented by construction and study of graphs on which species-area data for four of these same communities were converted to species-individuals curves, and superposed on a-curves. Two of these communities appear in Fig. 3. The following facts were noted: (1) The Reavis Woods curve nearly coincides with the curve $a = 5$ as far as the flex point at about 100 trees or 316 mlc., above which it gradually drops below this a-curve, being 1 species below it at 520 trees, 2 species below at 1200, and 5 species below at 5800 trees. (2) Each of 3 other curves in its lower course is nowhere far from a certain a-curve, but where it departs from this curve, the divergence is *upward*. The convex part of the community curve attains a height of 1 to about 4 species above the a-curve. In its upper course the community-curve gradually becomes less steep, crosses the a-curve, and continues the decline below it. (3) The place at which the upward trend away from the a-curve begins, varies in different communities. It is well below the flex point of the Brownfield and Philippia heath curves (at 45 plants or 359 mlc. for Brownfield, 35 plants or 3.9 mlc. for the heath). The upward divergence for the California bush is at 450 plants or 69 mlc., about at the flex point. (4) The community curves also display individuality in additional less-obvious characteristics.

One may tentatively conclude that the use of species-individuals curves for populations or areas *in the range below the flex point* is seldom likely to

lead to serious error. The description of a 1-acre or half-hectare plot of tropical forest with stated S and N gives one point for a species-area curve. From a-curves (or the similar arbitrary species-individuals curves often used in their place), additional S and N combinations for new points are readily obtained.
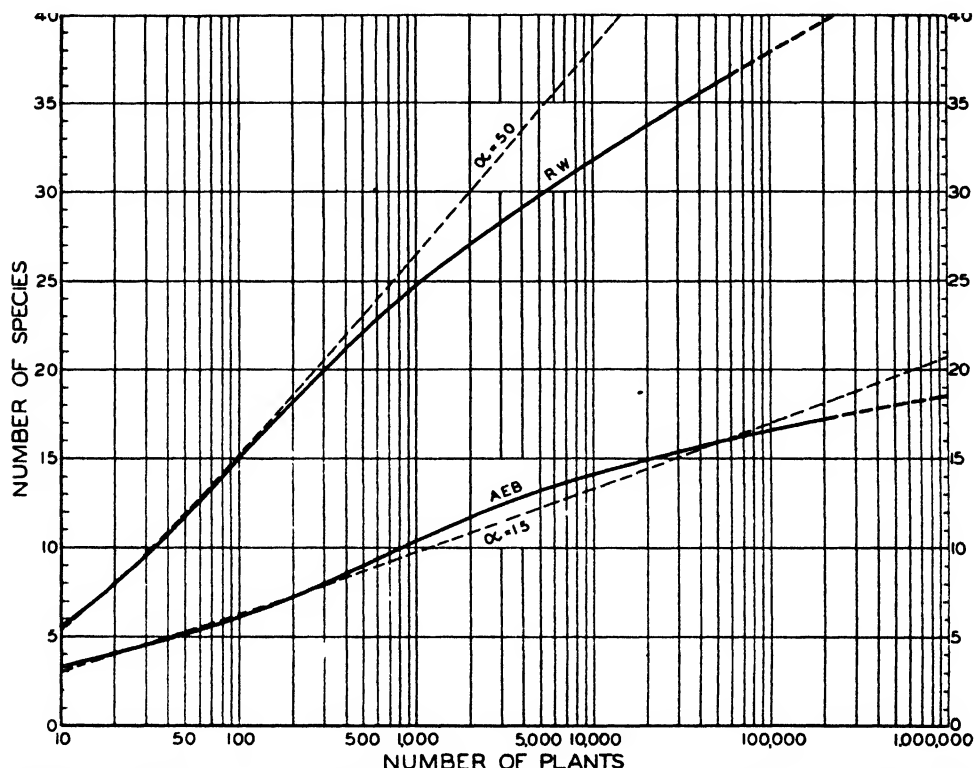

FIGURE 3. Relation of community curves (solid lines) to "constant-a" curves of the Fisher's series (broken lines). Both are species-individuals curves, the former adapted from species-area curves. The upper solid curve, for Reavis Woods, Indiana (data by Potzger *et al.*), is close to $a = 5$ up to about 150 trees, and thereafter diverges downward from it. In another more common type, the community curve makes its first departure, in the upward direction, from the a-curve which its lower course roughly follows. Its convexity brings it to a crossing of the a-curve, as shown. The second community example is *Artemisia-Eriogonum* bush at the southwest base of San Gabriel Mountains.

If the description dealt instead with 25 hectares, so large an area would fall on the convex part of a species-area curve, well above the flex point. The conversion method just mentioned cannot be used in this case.

In spite of the considerable individualities of the community curves, and of the lack of agreement between such curves and a-curves in their upper sections, the author believes that Fisher's series, with its rational explanation of relation between numbers of species and numbers of individuals, is almost certainly the basis upon which additional characteristics of communities of rooted plants are superposed. Some of these characteristics are probably common to all estab-

lished vegetation; others constitute the qualities peculiar to certain types or to individual stands.

The suggestion is offered that certain types of field data, as those for Corbet's and Williams' collections of insects, or even line surveys in vegetation, and aggregates of well-separated very small plots, are less refractory statistical materials, so far as amenability to treatment by Fisher's series is concerned, than are the progressively larger one-piece areas of rooted vegetation here dealt with. The phenomena of competition and domination, with tendencies to nearly exclusive occupation by the relatively few most successful species; other factors contributing to difficulties and failures of free migration; the aggregation or "clumping" of individuals of one species; all these presumably operate differently in many plant communities as compared with those assemblages of animals which are less fixedly tied to particular areas.

It may prove that unsmoothed species-individuals curves for all sorts of organisms in all types of environments will reveal numerous peculiarities of individual populations which will lead to further investigation of the peculiarities. The curves should be based on direct field observations for that specific purpose, on populations of graduated sizes. Fisher's series should be a useful means of detecting and judging the peculiarities of curves and of populations.

A recent article by Preston (1948) considers the applicability of Fisher's series to collections of insects, records of occurrence of birds, etc. In his summary (p. 283) : "Random samples of ecological or taxonomic assemblages indicate that the universes from which they are drawn have, at least approximately, the form of an ordinary Gaussian curve drawn upon a logarithmic base (a 'log-normal' curve). The sample has the same general form as the universe, but is decapitated."

RESULTS: REFERENCE AREAS AND THEIR SPECIES-NUMBERS

The areas and numbers of species as determined from about 240 species-area curves, are stated with extreme compactness in the tables which follow; but to give them meaning it is necessary to provide a background: character and location of the type of vegetation; by whom studied in the field, with citations of publications; habitat, leading species; partial statement of given data, of conversions employed, and of converted data serving as basis for the curve. Conversions, described in an earlier section, are shown by symbols:

C. Use of *curves,* species plotted against individuals, for a particular number of plants, or for a particular area.

E. To *effective* plot-size from nominal plot-size.

F. Use of *frequence* or constance data to find species-per-plot.

I. To *integral* equivalent area of compact proportions,.from separated plots or from long strip.

L. Conversion of tree-diameter *limit,* to standard of three inches and larger.

R. Use of *random* spotting to approximate space-distribution of plants and species.

For some of the communities or stands studied there is no published statement; brief descriptions are provided.

Results were obtained for three reference areas: Ar, smallest representative area with its species-number Sr; Am, minimum area (= 5 Ar), with its species-number Sm (usually between 1.44 and 1.5 Sr); and Af, fair-sized stand (= 50 Ar, or 10 Am), with its species-number Sf (= 2 Sr). It is not necessary to give all six of these numbers. One area suffices, Am, expressed in both milacres and in square meters. (1 milacre or mlc. = 0.001 acre, or 43.56 sq. ft., or 0.2471046 sq. m.) Ar and Af, if needed, are found from the simple ratios given.

Readers will find Ar adequate for many purposes, since it almost always includes all the more abundant and generally distributed species of a stand. It is probably as large as the minimal area which has usually been adopted.

Since the ratio of Sm to Sr is not constant, both these species-numbers are given. Sf, if needed, is 2 Sr. For communities with known density of plant individuals (which may be restricted to one stratum, one growth-form, or to tree-sizes above a stated limit), the number of plants per acre is also given. The symbol for plants per thousand milacres is N1000. Number per acre is part of the background rather than a result, but aids in appraising reference areas. and their species-numbers. Degree of dependability is also shown for each line of results. The number 1 indicates a solid basis of data, in many cases obtained for species-area purposes; a sufficient range of plot-sizes with directly-determined species-numbers. It is believed that two independent sets of observations so obtained within the same stand would agree within 10 or 12 per cent.

17

(See the two determinations for Trelease Woods in Table 2.) The number 2 suggests dependability intermediate between 1 and 3. The number 3 is used if the description gives only 1 or 2 areas or an aggregate of very small plots; if L-conversion is radical; if much dependence is placed upon C-conversions or upon assumption; or if the total sample is obviously inadequate. Some results with number 3 dependability may be less than 20% different from true values; on the other hand, they may range from half to twice the true value. Such results would be worthless if it were not for the fact that one of two apparently similar stands of the same type may have reference areas more than twice as large as in the other.

In setting forth results for particular stands or types, a table first summarizes results for each group of communities; the background follows the table. For forests, ground vegetation and tree-cover are considered in different groups. Data for trees are converted to a standard size-limit, 3″ +, (abbreviated form to designate all trees 3 inches d.b.h. or larger). Column headings signify: Am = minimum area; Sr = no. of spp. at Ar or smallest representative area; Sm = no. of spp. at minimum area; N1000 = no. of trees per acre (i.e., at 1000 milacres); D = degree of dependability.

TREES OF MID-LATITUDE FORESTS

TABLE 2. Old-Growth Mixed Deciduous Forests in Illinois and Indiana.

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Brownfield Woods, Ill.	4015	16 249	12.5	18.3	125	1
Trelease Woods, grid	3202	12 270	12.4	17.9	115	1
Trelease Woods, 12 plots	3337	13 504	12.4	18.2	126	1
S.e. of Palestine, Ill.	3019	12 218	13.8	20.3	160	2
Culled stand, Robinson, Ill.	2750	11 129	11.3	16.6	84	2
S.w. of Robinson	1302	5 269	17.8	11.5	155	2
Cox Woods, Indiana	2761	11 173	13.6	20.2	176	3
Reavis Woods, n. slope	1518	6 144	14.8	21.6	315	1
O'Hare Woods, n. slope	2563	10 372	13.9	20.6	172	1
Potzger's No. 37, s. slope	2680	10 846	15.8	23.2	223	1
Potzger's No. 39, s. slope	868	2	11.1	16.3	310	1
McCoy's R, Sullivan Co.	1968	7 962	15.8	23.2	231	2
McCoy's X, Greene Co.	1862	7 534	14.0	20.5	283	2
J, Jefferson Co.	2393	9 686	13.5	19.7	271	2
B, Jennings Co.	2697	10 915	10.1	14.8	138	2
Y, Daviess Co., bottomland	1542	6 239	18.3	12.3	241	2
S, Sullivan Co.	1674	6 774	7.2	10.6	183	2
W, Greene Co., flatwoods	1428	5 781	6.9	10.1	180	2
C, Jennings Co.	910	3 684	3.9	5.5	142	2
Q, s. Vigo Co.	2694	10 902	12.9	19.0	112	2

BROWNFIELD WOODS, N.E. OF URBANA, ILL. MESOPHYTIC PRAIRIE-BORDER TYPE. VESTAL AND HEERMANS (1945). 52-acre sample with 25 spp.; in 60-acre stand with notable surviving giant trees. *Acer saccharum* now most

abundant. *Quercus macrocarpa, Q. Muhlenbergii, Q. rubra* (northern red oak), 2 elms, 3 ash spp., *Tilia,* etc. 12 leading spp. No conversions.

TRELEASE WOODS, 1 MILE E. OF BROWNFIELD. MARBERRY, MEES, AND VESTAL (1936). Similar to Brownfield, but less well-drained. 27 spp. in 14.4-acre aggregate: 6.4-acre grid of 100-mlc. plots, + 10 well-separated oblong plots each 800 mlc. *Q. alba* is significantly absent from stands of this type. The second determination is from the 10 large plots plus 2 other 800-milacre plots within the grid of 64 100-mlc. plots.

MIXED MESIC STAND, ON LOESS HILLS S.E. OF PALESTINE, CRAWFORD CO., ILL. S. R. BRADLEY (1932). At edge of Wabash River valley. 22 spp. in 10 100-mlc. plots; in ca. 36 acres. Conversions: F (6.9 spp. per plot), I (to 5 acres). *Acer saccharum, Liriodendron, Fagus, Q. rubra,* + 2 spp. (i.e., 6 leading spp.).

CULLED STAND, OPEN AND DECADENT, CA. 14 ACRES, AT ROBINSON, CRAW-FORD CO. BRADLEY (1932). 4 leading spp., *Q. velutina, Prunus serotina, Q. alba, Q. imbricaria.* Neither mesic nor xeric. 15 spp. in 10 100-mlc. plots, 6 spp. outside plots. F (5.5 spp. per plot) ; I (to 4 acres).

FLATWOODS, CULLED, S.W. OF ROBINSON. BRADLEY (1932). Ca. 18 acres, with 16 spp. 3 leading spp., *Carya ovata, Q. imbricaria, Ulmus americana.* 14 spp. in 10 100-mlc. plots. F, I.

COX WOODS, ORANGE CO., S. IND. POTZGER, FRIESNER, AND KELLER (1942). Another notable remnant of virgin forest. 200 acres; ca. 60 acres in good condition, with ca. 28 or 29 spp. Leading trees *Acer, Fagus, Liriodendron, Juglans nigra, Q. alba, Fraxinus americana.* 18 spp. in 50 separated 100-sq.-m. plots (10-m. interval). Spp. per plot est. at 2.74. I-conversion (to 1581 mlc.).

REAVIS WOODS, AND OTHERS IN 5 MILES OF PLOTS SURVEYED BY POTZGER AND FRIESNER (1940). This survey in 5 counties south of the middle of Indiana consisted of alternate-plot strips of varying length and number in many stands. Plots are 10 × 10 meters (24.7 mlc.). Original field notes were generously made available for this species-area study. Data were thus found for various combinations of plots. Young trees of between 1-inch and 3-inch d.b.h. were omitted from the tabulations. The only conversion required was I, to integral equivalent area. — Reavis Woods is in Morgan Co. 389 trees of 22 spp. in 50 n.-slope plots. *Fagus, Q. alba, Acer, Carya* (3 spp.), *Q. rubra, Sassafras, Ostrya,* etc. Spp. per plot, 4.86. I, 50 plots to 1548 mlc. 3 intermediate plot-sizes. The basis for curves for the other stands was similarly estimated from these field data of Potzger and Friesner.

O'HARE ESTATE, 3 MILES W. OF METAMORA, FRANKLIN CO.; NORTH-SLOPE FOREST. POTZGER & FRIESNER. 19 spp. in 50 plots. *Fagus, Acer, Liriodendron: Cornus florida* abundant.

STAND No. 37 OF POTZGER AND FRIESNER. SOUTH-SLOPE FOREST, 3 MILES W. OF METAMORA. 24 spp. in 50 plots. *Fagus, Q. alba, Carya ovata, Acer, Fraxinus americana.*

No. 39 OF POTZGER AND FRIESNER. SOUTH-SLOPE FOREST, FRANKLIN Co., 3.5 miles e. of Metamora. 17 spp. in 50 plots. Presumably calcareous site. *Q. Muhlenbergii, Q. rubra, Carya ovata, Fraxinus americana, F. quadrangulata.*

SCOTT MCCOY'S STUDIES (1939) IN MIXED FORESTS, MOSTLY FLATWOODS. IN S.E. INDIANA (stands A to P, some in the district called "The Flats") AND IN S.W. INDIANA (stands Q to Y). R, X, J, & B are well drained. Y is at times flooded; S, W, C, & Q are poorly drained. Most of these forests are on light-colored clayey soils. Each stand table summarizes 20 100-sq.-m plots, mostly in 2 alternate-plot strips. From McCoy's 25 forests, the 11 chosen for this study illustrate wide variation in many respects, especially in degree of richness of composition. Young trees between 1- and 3-inch d.b.h. were subtracted from the stand tables, thereby reducing somewhat the number of species from the listed total. Conversions: C, I (from 2000 sq. m. = 494.2 mlc., to 616.7 mlc.).

STAND R. SULLIVAN Co. 18 spp. in 20 plots. Most highly mixed of the 11. *Acer rubrum, Q. velutina, Q. rubra, Q. alba, Ulmus fulva, U. racemosa, Carya laciniosa, Fraxinus americana,* etc.

X. GREENE Co. IN SAND-CLAY MIXTURE. PASTURED. 16 spp. in 20 plots. *Q. alba, Fraxinus americana, Carya ovata, Acer saccharum, Q. velutina, Ulmus Thomasii, Acer rubrum.*

J. UNDISTURBED. 14 or 15 spp. in 20 plots. *Q. alba, Carya glabra, Fagus, A. saccharum.*

B. UNDISTURBED. 10 or 11 spp. in 20 plots. *Fagus, Carya tomentosa, Liquidambar, Liriodendron, A. saccharum.*

Y. IN BLACK BOTTOMLAND LOAM. 10 spp. in 20 plots. *Quercus palustris, Q. bicolor, Fraxinus profunda, Ulmus Thomasii?* (reported as cork elm, *U. racemosa*), *Acer rubrum.*

S. FIRST OF THE 4 POORLY-DRAINED STANDS MENTIONED. 12 spp. in 20 plots. *Q. alba, Q. imbricaria, Q. palustris, Carya ovalis, C. ovata, Q. bicolor, Nyssa sylvatica.*

W. STAND WITH SOME DISTURBANCE FROM PASTURING AND CUTTING. 8 or 9 spp. in 20 plots. *Q. bicolor, Q. imbricaria, Q. palustris, C. ovata.*

C. SEVERELY PASTURED FLATWOODS. Poorest in composition: 5 spp. in 20 plots. *Fagus, Liquidambar, C. ovata.*

Q. STAND WITH SOME CUTTING. 13 or 14 spp. in 20 plots: fairly rich, considering that this has lowest density among the 11 stands. *Q. velutina, Carya tomentosa, C. ovata.*

TABLE 3. Other Deciduous Forests in Illinois and Indiana.

Stand	Am, mlc.	Am, sq. m.	Sr	Sm	N1000	D
Black oak, Illinois River dunes	1 144	4 630	2.9	4.3	93	3
Blackjack oak, Illinois River dunes	1 800	7 284	2.0	3.0	179	3
Stony Lonesome, Bartholomew Co., Ind.	1 044	4 227	8.5	12.3	332	2
Ridge-top forest, Brown Co.	1 050	4 249	10.4	15.1	283	2
McCoy's I, cutover flatwoods	718	2 907	7.5	10.9	634	2
McCoy's V, young stand, Greene Co.	799	3 234	6.0	8.5	364	2

BLACK OAK DUNE FOREST, ZIEGLER (1904). This and the next illustrate simple composition in poor sites. In many places one or both oak species invaded sand prairie between 1830 and 1900. For a species-area curve, 6 species are assumed in 9 acres. Conversion: R, to give 8 plot-sizes. *Q. velutina* the only leading sp. A few *Q. rubra* (n. red oak). Other species rare. Low density.

BLACKJACK OAK DUNE FOREST, ZIEGLER (1904). Some fire-swept stands of this type are very scrubby, only 7-10 feet to tops of crowns. Ziegler's 2-acre sample with 2 spp. is assumed to be expanded to 16 acres with 4 spp. Conversion, R. *Q. marilandica* with $\frac{1}{4}$ to $\frac{1}{3}$ as many *Carya cordiformis*.

XERIC MIXED STAND AT STONY (OR STONEY) LONESOME, BARTHOLOMEW CO., IND. AREA NO. 26 OF POTZGER AND FRIESNER (1940). Stony siliceous soil, south slope. 11 spp. in 20 100-sq.-m. plots. High density, trees mostly small. *Q. alba, Q. montana, Q. velutina, Fagus*. I, from 2000 sq. m. to 597 mlc.

RIDGE-TOP FOREST, 3 MILES E. OF NASHVILLE, BROWN CO. AREA NO. 7 OF POTZGER AND FRIESNER. They give 4 other small ridge-top samples, one (No. 45) with density of 425 trees per acre. In No. 7, 14 spp. in 22 plots in 1 alternate-plot strip. *Q. velutina, Q. alba, C. ovata, Fraxinus* sp., many small *A. saccharum*. Many species for the area, attributed to narrow site between two extensive forested slopes of different types. I, from 543 mlc. to 830 mlc.

McCoy's STAND I, JEFFERSON CO. 28-year stand replacing flatwoods cut in 1910. 10 or 11 spp. in 20 plots. *Liquidambar, Nyssa, Q. alba*. Highest density among the 11 stands. Representative for a young even-aged mixed forest.

McCoy's V, GREENE CO. Very young forest of fairly high density. A bottom-land type in black loam. 8 spp. in 20 plots. *Q. palustris, Acer saccharinum, Fraxinus profunda, Ulmus racemosa*.

NORTHERN PINE FORESTS

	Am. mlc.	Am. sq. m.	Sr	Sm	N1000	D
Pinus resinosa, Trout Lake, Wis.	678	2 743	6.3	9.2	372	2
Pinus strobus, near Wolf Lake, Wis.	860	3 480	5.8	8.4	255	1

NORWAY PINE FOREST ON THE POINT, TROUT LAKE, VILAS CO. N. WISCONSIN. J. E. POTZGER (1946). The computations and curves for this stand and the

next were made from Potzger's original field enumerations. The article in which his descriptions of these stands are included has since appeared (Potzger, 1946). Data for this stand, the Point Forest, are on pp. 213, 215, 220, 222, 235 (figs. 2 and 3). — Nearly undisturbed stand, ca. 40 acres. 9 or 10 spp. in 20 100-sq.-m. plots, *P. resinosa* dominant, in every plot, to 24″ d.b.h. *P. strobus* locally abundant, in 9 plots, 3-19″, mostly small. *Acer saccharum, A. rubrum, Q. rubra* (n. red oak), *Betula papyrifera;* 1 tree each of *Abies* and *Thuja.* Conversion: I, to 618 mlc.

WHITE PINE FOREST AT DAIRYMEN'S COUNTRY CLUB, BETWEEN BIG CROOKED AND WOLF LAKES, VILAS CO., WIS. POTZGER (1946). Data for this remarkable stand are on pp. 214, 220, 221, 224, 225, 236 (fig. 4).—Undisturbed stand, ca. 80 acres. 9 spp. in 50 plots, mostly in 2 strips. *P. strobus* dominant, in 46 plots; to 25″ d.b.h. *P. resinosa* in 35 plots, in places codominant, to 23″ d.b.h. *Acer saccharum, Abies balsamea, Acer rubrum;* 3 trees of *Tsuga.* Conversion: I, to 1736 mlc. — A later treatment of the ground layer, prepared from Table 23 in Potzger's article, appears in the section on stratified and mixed communities.

The fact that conifers grow to sizable trunk diameters with narrower crowns and smaller ground-space per tree than deciduous dicots, is reflected in the high density of these two stands (as compared with mature deciduous timber). This characteristic appreciably reduces the reference areas.

SCLEROPHYLL OAK WOODLAND, SOUTHERN CALIFORNIA

	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
60-yr. stand, Fern Canyon, 4900 ft.	319	1290	5.8	8.7	1 or 2

EVERGREEN OAK WOODLAND, SAN GABRIEL MTS. U. S. FOREST SERVICE, 1935. Fern Canyon is tributary to San Dimas Canyon in the northeastern part of San Dimas Experimental Forest of California Forest and Range Experiment Station. Field notes and plot-maps were made in 1935 by R. W. WIESE & E. F. WALLIHAN, and were made available for this study at the Glendora Office of the Forest Service through the generosity of the Station and with the kind help of Mr. Jerome S. Horton. An earlier forest was destroyed by fire ca. 1875, and was succeeded by chaparral. This has been developing into forest again. The vegetation is a mixture of several growth-forms, shrubby oaks, large rounded oaks of small-tree stature, young trees of *Pseudotsuga macrocarpa* (only seedlings are in the plots), chaparral shrubs and bushes of several types. Two oak species are strongly dominant, *Q. Wislizeni* var. *frutescens* and *Q. chrysolepis.* They alternate rather than intermingle. The shrubs and bushes are very infrequent, only one, *Ceanothus integerrimus,* approaching 30% occurrence in plots. Four species of next, though minor importance, are *Garrya Veatchii, Rhamnus californica* var. *ilicifolia, Penstemon ternatus,* and *Lonicera subspicata.* — The 99 plots, each 10 feet square, are in 3 groups separated by intervals of about 20 feet. Plots in each group are contiguous. They were established to study runoff

and erosion: the 9 down-slope strips are designated S.R.E. strips 341 to 349. Combinations of them provided 11 different plot-sizes. Since most of the oaks had several small stems, a 2-inch diameter limit was adopted. If a 2-inch stem *or* more than half of a crown occurred in the plot, that oak species was counted. The same convention, except that stem-diameter was disregarded, was applied to shrub and bush species. Recently-dead shrubs of *Ceanothus,* and seedlings of *Pseudotsuga,* were arbitrarily counted. Mean species-number per single 2.3-mlc. plot is 1.47. 8.0 spp. occur in 177 mlc.; 8.0 spp. again in all 99 plots (= 227 mlc.) As might be expected, the reference areas are smaller than for forest, larger than for all but one of the chaparral and other shrub or bush vegetations studied.

SUBTROPICAL FORESTS

TABLE 4. Subtropical Forests, and Low-Latitude Mountain Forests.

Stand or type	Am, *mlc*	Am, *sq. m.*	Sr	Sm	N1000	D
Eugenia–Vaccinium, Bataan	280	1 133	12.9	19.3	747(?)	3
Mossy forest, Mt. Maquiling	764	3 090	12.1	18.1	332	2?
Mossy forest, G. Belumut, Johore	510	2 063	12.4	18.6	604(?)	3
Mixed subtrop. forest, Mauritius	1575	6 377	32.5	49.0	778(?)	2
Shorea–Plectronia, Bataan	1856	7 508	54.3	79.6	782	3
Quercus–Neolitsea, Mt. Maquiling	3441	13 920	44.5	65.2	257	3

EUGENIA–VACCINIUM FOREST, BATAAN PENINSULA, LUZON, 900-1265 M. ELEV. H. N. WHITFORD (1906: 652-666). 8 stations, 150 to 360 sq. m.; aggr. area 1792 sq. m., with 693 trees 3 m. high and taller (none reached 15 m.), in 65 spp. Sites differ. About 15 leading spp. (fewer in 1 plot): *E. congesta, E. acuminatissima, Acronychia laurifolia, Quercus* sp., *V. Cumingianum, Clethra lancifolia, V. Jagori,* etc. Plots individually spotted on species-area graph; curve drawn through swarm of points in same form as for less uncertain mossy forest on Mt. Maquiling. Conversion to 3″ limit suggests for same area (443 mlc.), 339 trees. A one-piece area of this size and of uniform site, probably has only 21 spp. Station A, largest (88.4 mlc.), most exposed, xeric, and steep, on volcanic peak with some fine soil, and at 900 m. elev., is closest to average condition represented by the curve. Station D is richest (Sm ca. 23); B is poorest (Sm ca. 17).

MOSSY FOREST, MT. MAQUILING, LUZON, 1020 M. ELEV. W. H. BROWN (1919: 98-109). 10 plots, each 5 × 10 m., presumably near one another. Size-limit, 1 m. height (but if it were 4 m., only 1 sp. fewer). 157 such trees of 17 spp. in 123.6 mlc. Brown also noted 21 spp. in 2500 sq. m. Only 3 spp. exceed 10 m., only 1 in 12-14 m. height-class. Abundant spp. (only 1 exceeding 8 m.) are *Astronia lagunensis, Clethra lancifolia, Cyathea caudata, Melastoma polyanthum, Itea maesaefolia.* L-conversion to trees of 5.25 m. ht. or 3″ d.b.h. and larger: 4.1 trees of 3.1 spp. in 12.36 mlc.; 61.5 trees of 12.6 spp. in 173 mlc. (1-piece area equiv. to 10 plots); 246 trees of 18 spp. in 741 mlc. Wide, distorted

crowns and loading of epiphytes are responsible for relatively low density. Perhaps this forest, like California oak woodland, can hardly be compared with ordinary "high forests."

Mossy forest, Gunong Belumut, Johore. Ca. 915 m. elev. near summit. R. E. Holttum (1924). Usable through density comparison with mossy forest on Mt. Maquiling for woody plants taller than 2 m. One 400-sq.-ft. plot and enumeration of larger trees. Ca. 9 leading spp., incl. 4 *Eugenias, Calophyllum canum, Podocarpus neriifolius*. Conversions suggest 4 spp. at 9.18 mlc., and 13.4 spp. at 129 mlc. Curve and results uncertain. A less extreme type than the preceding.

Mixed subtropical forest, Mauritius. 550 m. elev., above Black River gorges. Vaughan & Wiehe (1941). 1710 trees of 52 spp. (10-cm. diam. limit), in 10 separated plots, each 50 × 20 m., within one 800-ha. stand. Ca. 15 leading spp.: *Eugenia glomerata*, "Bois Caf-caf" (*Euphorbiaceae*), *Mimusops maxima, Aphloia theiformis, Elaeodendron orientale, Nuxia verticillata*, etc. Conversions: L, C. Est. spp. per plot, 31; 53 spp. in 2471 mlc. Notably high density. Type "probably akin to Tropical Lower-Montane Evergreen Rainforest of Burtt Davy."

Shorea–Plectronia forest, Bataan. 450-900 m. elev. Whitford (1906: 642-645). 7 stations, 252 to 1440 sq. m., aggr. area 887 mlc. Sites differ. At greater elev. trees are smaller and density higher. 1011 trees 4 m. + (4 m. tall and taller) in 91 spp. Perhaps 13 leading spp. *Shorea polysperma* and other dipterocarps form 16% of stand. *Plectronia viridis* is the abundant sp.; dominates shady 2d story. Other notable spp.: *Memecylon edule, Calophyllum Whitfordii, Hopea acuminata, Thea montana, Eugenia* spp., *Cinnamomum mercadoi, Agathis philippinensis*. Stations are individually spotted on graph. Conversions, L: ratio is 192 trees 4 m. + to 132 trees 3″ +; C; l, a 1-piece area 2.5 × the aggregate is assigned same no. of spp., 83.9. — These 7 stations are given in Whitford's Table 19. In Table 20 are 4 stations of a large-tree variant, with density 501 instead of 782. These 4, with Station B from Table 19, fall almost on the curve for Brown's *Quercus–Neolitsea* association.

Quercus–Neolitsea forest, Mt. Maquiling. 700 m. elev. Brown (1919: 76-, 96). Plot is 0.25 ha., with 577 trees and 71 spp. 1 m. ht. +; or 138 trees and 38 spp. 10 cm. diam. +. This is also "midmountain forest, moist-tropical, evergreen, 2-story." Perhaps, like the preceding two, it is transitional between tropical and subtropical. Leading top-story spp. include *Quercus soleriana, Cratoxylon celebicum, Neonauclea calycina, Weinmannia luzoniensis*, and *Ficus* spp. Second-story trees include *Oreocnide trinervis, Neolitsea villosa*, and *Saurauia luzoniensis*. Tree-ferns, rattans, and *Freycinetias* are prominent. Conversions, L and C: to 159 trees and 40 spp. 3″ +, at 618 mlc. Trend of curve judged from curve for preceding type.

TROPICAL FORESTS: PHILIPPINES, MALAYSIA

TABLE 5. Tropical Forests: Philippines, Borneo, Singapore, Ceylon.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Dipterocarpus–Shorea, Bataan	4 700	19 020	61.3	91.2	213.6	3
Dipterocarp forest, Mt. Maquiling	5 288	21 400	60.5	90.7	207.2	3
Anisoptera–Strombosia, Bataan	5 639	22 822	65.5	99.5	109.3	2
Lower Forest, Mt. Maquiling	6 560	26 547	58.5	86.4	183.2	3
Culled Dipterocarp, Mt. Maquiling	4 290	17 361	54.3	80.1	137.3	3
"Over-cut" forest, Mt. Maquiling	6 900	27 923	50.6	75.1	151.4	3
Dense parang, Lamao, Bataan	2 943	11 910	55.5	82.2	684.4	3
Grassy parang, Mindoro	21 400	86 603	26.3	38.8	54.6	3
Mixed rain-forest, Mt. Dulit	10 793	43 677	95.6	143.3	140.0	3
Marudi heath-forest, Sarawak	6 265	25 354	52.3	76.8	187.3	3
Koyan heath-forest, Sarawak	6 545	26 487	51.4	75.3	176.1	3
Southeast Borneo: Tanah Boemboe	6 550	26 507	61.3	91.6	130.7	3
Southeast Borneo: Pleihari	7 835	31 707	41.7	62.6	110.1	3
Secondary forest, Singapore	1 320	5 343	33.2	49.3	471.5	1
Sinharaja Forest, S.w. Ceylon	7 125	28 834	39.0	57.0	244.0	3

DIPTEROCARPUS–SHOREA FOREST, BATAAN. 340-410 M. WHITFORD (1906: 637-). Main plot on ridge at 340 m.: data by T. E. BORDEN. 1160 trees 4 m. + (ht.), 85 spp., in 8325 sq. m. 4 smaller plots at 410 m., 1 at upper limit for type. Top-story spp. are *Dipterocarpus grandiflorus, Shorea polysperma* and *S. contorta, Santiria nitida, Calophyllum Wallichianum,* and *Eugenia glaucicalyx.* L, C: 757 trees 3″ +, 77 spp. on 2057 mlc.

DIPTEROCARP FOREST, MT. MAQUILING. 450 M. BROWN (1919: TABLES 2-10). BROWN & MATHEWS (1914: TABLE 12). Main plot .25 ha., with 107 trees 10 cm. +, 43 spp. 22 top-story spp., incl. 3 dipterocarps: *Parashorea plicata, Shorea guiso, Hopea acuminata.* Also notable: *Celtis philippinensis, Canarium* (4 spp.), *Eugenia* (4 spp.) ; in 2d story: *Diplodiscus paniculatus, Dillenia philippinensis, Ficus* (4 spp.). 7 spp. in 3d story: 4 spp. over 2 m. high in 4th story as part of undergrowth. L, C: 128 trees 3″ +, 49 spp., in 618 mlc.

ANISOPTERA–STROMBOSIA FOREST, BATAAN. 80-250 M. WHITFORD (1906: 403-). Main plot 170 × 60 m. on diversified slope has 896 trees 4 m. +, in 120 spp. Plot on terrace of Lamao River, ca. 8000 sq. m., has 328 trees 4 m. +, in 92 spp. 6 other plots, 600 to 1500 sq. m. This richest forest of the Lamao Reserve occupies the zone above the lowest (the basal forest is *Bambusia–Parkia*). 31 top-story spp., incl. *Shorea* (3 spp. listed in preceding types), *Dipterocarpus vernicifluus, Anisoptera Vidaliana, Euphoria cinerea, Mangifera altissima.* In lower stories: *Strombosia philippinensis, Gnetum gnemon, Diospyros pilosanthera.* L, C (terrace plot) : 216 trees 3″ +, 79 spp., in 1977 mlc.

LOWER FOREST, MT. MAQUILING. BELOW 300 M. ELEV. BROWN & MATHEWS (1914: 446-). On 1 ha., 403 trees 10 cm. +, ca. 63? spp. ("miscellaneous spp." not segregated). This type should be at least as rich in spp. as the main diptero-

carp forest just above. Ca. 9 leading spp.: *Diplodiscus paniculatus, Parashorea plicata, Diospyros* sp., etc. L, C: 453 trees 3″ +, 70? spp., 2471 mlc.

CULLED DIPTEROCARP STAND, MT. MAQUILING. 200 M. ELEV. BROWN (1919: 61-75). Plot .25 ha.: 887 trees 1 m. high and above in 129 spp.; 75 trees 10 cm. +, 42 spp. Of these 42, 10 are top-story spp., 28 are 2d-story, and 4 are 3d-story. L, C: to 93 trees 3″ +, 48 spp.

"OVER-CUT" FOREST, MT. MAQUILING, 140 M. ELEV. BROWN & MATHEWS (1914: 444). Top story had been cut away. On 1 ha., 319 trees 10 cm. + diam., ca. 55? spp. (misc. spp. not segregated). *Diplodiscus* the only abundant spp.; *Garcinia binucao, Planchonia spectabilis, Dracontomelum Cumingianum*, etc. L, C: to 374 trees 3″ +, 60? spp.

DENSE PARANG, LAMAO, BATAAN. 35 TO 70 M. ELEV. WHITFORD (1906: 391). Parangs are secondary forest, following cutting. They differ greatly in composition and otherwise, depending on history and surroundings. 3 small plots, 2 to 3.5 km. inland, in lowland or *Bambusia–Parkia* formation. In 480 sq. m., 131 trees 4 m. +; 29 spp. 12 to 19 spp. in any 1 plot. Tall trees include *Aphananthe philippinensis, Anisoptera, Buchanania florida, Macaranga bicolor, Parkia Roxburghii*. L, C: for av. plot, 12 spp. in 39 mlc. Trend of curve is close to that of culled dipterocarp stand. Density is about 3 times that of old-growth forest.

GRASSY PARANG, NEAR MAUJAO, MINDORO, P. I. M. L. MERRITT (1908: 39). Many parangs in Mindoro are scattered-trees-in-grass. This stand, with trees more closely spaced than is usual, is ¼ to ⅓ stocked. 1.73 ha., with 203 trees 10 cm. +, in ca. 25? spp. 7 or 8 leading spp., incl. *Sarcocephalus cordatus, Lagerstroemia speciosa, Barringtonia* sp., *Mitragyne diversifolia*. Other, chiefly parang spp.: *Albizzia procera, Antidesma* spp., *Grewia tiliaefolia, Bombycidendron Vidalianum*. L, C: on 4.27 acres, 233 trees 3″ +, 26.3? spp. Estimate for 1 acre: 55 trees, 15.5 spp. Reference areas prove to be extremely large. This illustrates the common and rather obvious influence of density: if trees are farther apart, larger area is required. Note contrast in size of Am as between this and the dense parang.

MIXED RAIN-FOREST, MT. DULIT, SARAWAK. 100-200 M. ELEV. P. W. RICHARDS (1936: 21, 359). Main plot near Kapah River, 400 ft. square (1.418 ha., = 3672 mlc.), on steep side of ridge. 261 trees 8″ +, 98 spp. 2 profile strips, each 200 × 25 ft., on ridge-top and side-slope. Perhaps 16 leading spp. (listed under native names) incl. a sp. of *Shorea?* and one of *Dialium?*. Conversions: L & C: 513 trees 3″ +, in 112? spp., on 3672 mlc. Moderate density; rather large reference areas.

HEATH-FOREST, MARUDI PLOT, SARAWAK. A FEW METERS ABOVE SEA-LEVEL. RICHARDS (1936: 28, 359). At edge of sandy plateau. 350 trees 8″ +, of 56

spp., on 3672 mlc. Of 7 abundant spp., 3 are dipterocarps. Others are *Agathis borneensis* and *Ternstroemia aneura*. L & C: 688 trees 3″ +, 69? spp. Somewhat higher density and less rich composition than in mixed forest of the same district are characteristics of heath forests (also known as "white-sand forests," "Wallaba forests," or moist-climate "caatingas"). These occupy similar sites in many tropical regions. Soil is sterile and leached; usually on well-drained uplands. In some of these forests, one species is most numerous or is dominant. *Agathis* forms notable stands in the Marudi district.

HEATH FOREST, KOYAN PLOT, SARAWAK. CA. 750 M. ELEV. RICHARDS (1936: 28, 359). Deep, narrow, moist valley, of upper Koyan River, 329 trees 8″ +, in 55 spp., on 3672 mlc. Ca. 8 important spp., incl. *Agathis;* a relative of *Melanorrhoea; Casuarina sumatrana;* an oak or near relative; *Calophyllum?* (2 spp.) ; a dipterocarp. L & C: 647 trees 3″ +, in 67? spp.

SOUTHEAST BORNEO: TANAH BOEMBOE. VAN DER LAAN (1926, 1927), (AS REPORTED BY MILDBRAED (1930A: 55-56). Original not seen. Mildbraed's brief summary gives number of large-diameter trees, and number of species they represent, in each of 7 sample plots (presumably 1 hectare). They are in 4 localities. For the first (Tanah Boemboe), figures are given for mean, maximum, and minimum degrees of richness of composition. Diam. limit is 30 cm. for *Eusideroxylon Zwageri* and several important dipterocarps, and 40 cm. for other spp. For Tanah Boemboe (max.), "mean diam. limit" is est. to be 31 cm. (12.24″). For Pleihari (max.), est. is 32 cm. (12.63″). Only these 2 enumerations were considered amenable to conversion to 3″ diam. limit.

For TANAH BOEMBOE (MAX.), 91 trees 31 cm. +, in 47 spp. occupy 1 ha. Conversions, L and C: to 130.7 trees 3″ +, in 55.1 spp., on 1000 mlc. On 300 mlc., 28.5 spp.; on 100 mlc., 11.6 spp. Actual density of trees, 3″ +, may be somewhat higher, without change in no. of spp.

PLEIHARI. VAN DER LAAN, IN MILDBRAED (1930A: 55-56). Max. and mean data are given. For Pleihari (max.), 73 trees 32 cm. +, in 29 spp., on 1 ha.; to 110.1 trees 3″ +, in 34.8 spp., on 1000 mlc. On 300 mlc., 18.7 spp., on 100 mlc., 8.6 spp.

SECONDARY FOREST, SINGAPORE. I. H. BURKILL (1919). Part of the Botanical Garden, on n. w. slope. Original forest was mostly cleared in 1869; weed trees grew up after ca. 1888, and were 30 years old in 1918 when 2 acres were cleared, and about ⅓ acre tabulated. 943 trees 3″ + in 2 acres; ca. 148 trees 3″ + of ca. 37 spp. in 314 mlc. (2 plots). 6 or 7 leading spp: *Arthrophyllum diversifolium, Rhodamnia trinervia, Symplocos fasciculata, Adinandra dumosa, Durio zibethinus, Elaeocarpus stipularis, Ficus polysyce.* Also *Cinnamomum iners, Artocarpus* spp. High density, small reference areas. I ; to 157 trees in 333 mlc.

SINHARAJA FOREST, S. W. CEYLON. 579 M. ELEV. J. R. BAKER (1938). In largest remaining virgin tract of 90 sq. miles. Count of trees of girth 4 ft. or more at 4 ft. height, on half-acre squares. (Corresponds to size limit of 14.65" d.b.h.) 25 trees in 13 spp. Spp. include *Durio zeylanicus, Myristica dactyloides, Calophyllum* (2 spp.), *Doona, Palaquium, Mesua, Mangifera zeylanica.* L & C: to ca. 122 trees 3" +, in ca. 26 spp. Large reference areas; relatively poor in species composition.

TROPICAL FORESTS: WEST AFRICA

TABLE 6. Tropical Forests: West Africa.

Stand or type		Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Liberia: Evergreen Forest	Strip 1	9 478	38 334	51.2	77.6	91.4	2
	Strip 2	9 000	36 422	44.3	66.0	127.8	2
	Strip 3	10 430	42 209	47.6	69.2	122.4	2
Southern Nigeria:							
Mixed rain-forest	S. P. 1	12 345	49 959	30.4	45.0	189.1	2
	S. P. 2	10 730	43 423	39.4	59.4	244	1
	S. P. 3	9 195	37 211	53.4	79.2	181.7	1
Swamp forest	S. P. 4	10 715	43 362	34.0	50.0	167.3	1
Fernando Po: Mixed rain-forest		5 690	23 027	20.3	29.6	103.6	2
Kamerun: Jentsch; Primary forest							
Ngongnkeng	Plot VIII	5 592	22 628	108.8	162.2	251	2
Johann-Albrechts Höhe	II	6 065	24 544	89.0	132.6	202.4	2
Mundeck	V	6 142	24 856	78.7	117.2	242.9	2
Mujuka	VI	3 890	15 742	43.3	65.6	137.6	3
Bekili	III	5 115	20 700	61.0	91.4	217	2
Manoka	XII	11 550	46 741	24.4	36.9	136.5	3
Secondary forest (Kamerun)							
Njabi	XI	5 585	22 602	100	148.3	218.9	2
Johann-Albrechts Höhe	I	5 581	22 587	135.5	203.1	272.9	3
Bekili	IV	4 203	17 009	49.9	73.3	169.1	2
Likomba (Kamerun)	Plot VII	5 315	21 509	27.0	39.3	110?	3

LIBERIAN EVERGREEN FOREST, DUKWIA REGION. G. P. COOPER, 3D (1931). The study is based on 3 strips of half-acre plots. No. 1 has 16 plots, along southern side of a stand of "heavy bush," from which some trees have been cut. On 8 acres, 864 trees 2" +, in 89? spp. Strip No. 2, 16 plots, extends north from an end of Strip 1. It is in heavy to medium bush, with a few openings. 1253 trees 2" +, 74 spp. Strip No. 3 has 20 plots, and is in a different location. It includes some swampy spots with inferior growth. The largest trees are in No. 3. On 10 acres, 1448 trees 2" +, 81 spp.—In the 3 strips, 9 or 10 large-tree spp. are notable, incl. *Anopyxis ealaensis, Berlinia* spp., *Canarium Schweinfurthii, Erythrophleum guineense, Lophira alata, Pentadesma butyracea.* About 19 small-tree spp. are abundant: spp. of *Carapa, Cola, Diospyros, Macrolobium, Polyalthia, Strombosia, Vitex, Xylopia,* etc. —Conversions: L & C, I. In strip 1, to 914 trees 3" +, of 78 spp., in 10 acres. In strip 2, to 1278 trees 3" +, of 67 spp., in 10 acres. In strip 3, to 1469 trees 3" +, of 71 spp., in 12 acres.

MIXED RAIN-FOREST, SOUTHERN NIGERIA. P. W. RICHARDS (1939). In each
of 4 types, Richards listed trees 4″ + on a sample plot 400 ft. square, divided
into 4 strips 100 ft. wide. He also tabulated 2 clear-felling strips, each 200 ×
25 ft. (in plots 1 and 2). S. P. 1 is ca. 8 km. n. of Akilla, and is on nearly level
upland, not far from Erioloma River. 606 trees 4″ + in 34? spp. About 8
leading spp. *Berlinia auriculata* and *Scottellia kamerunensis* have the most large
and fair-sized trees. *Diospyros insculpta* and *D. confertiflora, Rinorea* sp., and
Picralima umbellata, mostly smaller, are abundant. Conversions, L & C: to
695 trees 3″ +, of 35 spp., in 3672 mlc. For each of 3 smaller areas, species-
numbers were proportioned from composite of values read from Richards'
species-area curves for the other 3 types.

RICHARDS' S. P. 2. NEAR ELUJU VILLAGE, ca. 5 km. n. of Akilla, on low tongue
of nearly level dry land between 2 swamp areas. Plot is divided into 4 strips
100 ft. wide, the basis for Richards' species-area curve. 781 trees 4″ + in ca.
46 spp. Ca. 8 leading spp. *Erythrophleum micranthum* is no. 1 among large-tree
spp. *Casearia bridelioides, Diospyros confertiflora,* and *Scottellia* also have some
large trees. *Rinorea oblongifolia, Strombosia pustulata,* and *D. insculpta* are the
abundant small trees.—L & C: to 896 trees 3″ +, 47.5 spp., in 3672 mlc.
Species-numbers for 1, 2, and 3 100-foot strips were read from Richards' curve.
As converted for trees 3″ +, they are 26.7, 37.3, and 42.3 spp.

RICHARDS' S. P. 3. IN BENIN PROVINCE, WITHIN OKUMU FOREST RESERVE.
Ca. 50 km. w. of S. P. 1. The richest of Richards' mixed-forest plots. 582 trees
4″ +, in ca. 65 spp., in 3672 mlc. Not so many large and middle-sized trees as
in S. P. 1. Spp. of *Strombosia* are most abundant, as are *Diospyros* (2 spp.), and
Pausinstalia brachythyrsa. "Apako" (*Annonaceae*) has some large trees. Also
notable are *Garcinia ovalifolia, Sapium ellipticum* and *Scottellia.* Ca. 11
leading spp. — L & C: to 667 trees 3″ +, ca. 67.3 spp., in 3672 mlc. *S* for 1, 2,
and 3 strips (derived from Richards' curve): 33.2, 50, and 60.5 spp. — Mixed
rain forests in both Liberia and S. Nigeria appear to be only moderately rich in
species composition. Density is low to medium. Reference areas are compar-
atively large. Cooper considers the forests he studied to be "second-class ever-
green forest."

FRESHWATER SWAMP FOREST, IJEBU PROVINCE. RICHARDS' S. P. 4. Within
Shasha Forest Reserve. Also 400 ft. square, in 4 strips. 536 trees 4″ +, in ca.
39 spp. Numerous large trees, especially of *Mitragyna stipulosa* and *Spondi-
anthus* spp. Also notable: *Alstonia congensis, Casearia bridelioides,* and *Sarco-
cephalus nervosus.* No marked abundance for any of the small-tree spp. — L & C:
to 614 trees 3″ +, in 40.3 spp., in 3672 mlc. *S* for 1, 2, and 3 strips (derived
from Richards' curve), 23.5, 32.5, and 36.7 spp.

MIXED FOREST, FERNANDO PO. H. BURCHARDT, REPORTED BY J. MILDBRAED
(1933). Burchardt made a detailed survey of plants in 1 hectare on this island

which is close to the coasts of both S. Nigeria and Cameroon. Tree diam. was measured at 1-meter height. The description leaves doubt whether more than one or a few trees a little smaller than 10 cm. are present. One reads into a sentence by Mildbraed (on p. 949) that some smaller stems may not have been measured. The count gives 237 trees 10 cm. $+$ in 23 spp. Of 9 or 10 large-tree species, *Pycnanthus kombo* and *Chrysophyllum africanum* are abundant. 3 species attain 130-cm. diam.; 7 spp. reach or exceed 80 cm. Of 13 or 14 middle-sized or small tree spp., *Strombosia grandifolia* and *Monodora myristica* are abundant. *Strombosia* thrives in deep shade. It has 105 of the 237 trees and is uniformly distributed over the plot.—Conversion (L & C) suggests a maximum of 256 trees 3″ $+$, in 25? spp., on 2471 mlc.,—and 10.4 trees of 5.2 spp. on 100 mlc. — Mildbraed remarks on the low proportion of species to trees (Mischungsquotient) in comparison with Jentsch's Kamerun plots, and correlates it with strong domination by *Chrysophyllum, Pycnanthus,* and *Strombosia.* These species make up $\frac{3}{4}$ of the whole (by number): unusual in a tropical mixture. This factor and the rather low density increase size of reference areas.

PRIMARY MIXED RAIN-FOREST, KAMERUN. JENTSCH (1911). This much-cited study comprised surveys of half-hectare plots in 8 localities. (In 3 of these, and a 9th station, secondary forests were also enumerated.) Plots II, III, V, & VII were completely tabulated for all trees 7 cm. diam. and larger. Half of Plot VIII was thus tallied; for the other half, and for all of plots VI, X, and XII, the count included no trees smaller than 20 cm. The 7-20-cm. class was estimated for these areas from the complete tallies for other plots. Species-numbers are thus uncertain for some localities. Jentsch's account lists species for only one plot, V, using native names (for a few kinds, scientific names also).

NGONGNKENG: PLOT VIII (P. 24). 1 km. s. of "Hauptlingsdorf Ngongnkeng auf lehmem bis steilen Nordhang." Elev. at the village is 590 m. Soil is laterite overlying gneiss. Tree-height is less than in most rain-forest. On the half-plot tallied, 75% of the stems are 7 to 20 cm. diam. Jentsch's est. for whole plot: 334 trees 7 cm. $+$, in 116 spp. on .5 ha. L & C: to 310 trees 3″ $+$, in 108 spp., on 1235.5 mlc. This type shows at the minimum area more species (162), than any other *primary* tropical forest among 31 studied. It is first also in no. of spp. on one acre: 104. A factor in this richness of Jentsch's Plot VIII is its somewhat unfavorable site, contributing to fairly high density. Its Mischungsquotient for trees 3″ $+$ *at 1 acre* is 1:2.405 (1 sp. to 2.405 trees). In this measure of richness of composition, Plot VIII is surpassed by 3 secondary forests, by Whitford's *Anisoptera-Strombosia* (the richest: M. Q. $=$ 1:1.751) and by Cooper's Liberia Strip No. 1 (1:2.343).

JOHANN-ALBRECHTS HÖHE: PLOT II (PP. 20-21). Ca. 2 km. n. e. of Johann-Albrechts Höhe station, on a s.e. slope. Lateritic loam over Schiefergestein (slate or schist). The 7-20-cm. size-class numbers only 51.5% of the stand. 260 trees 7 cm. $+$, in 91 spp.—L & C: to 250 trees 3″ $+$, in 88 spp. on 1235.5 mlc.

MUNDECK: PLOT V (PP. 21-23). In large expanse of nearly untouched forest near Mundeck station (km. 73 on north line of railroad). Level to east-sloping, "auf milden Lateritboden." 323 trees 7 cm. +, in 81 spp. This is the plot with detailed listing. 4 spp. are abundant, with 37, 33, 27, and 17 trees. 3 spp. (one is *Uapaca Staudtii*) have 9 trees each. 3 spp. (one is *Alstonia congensis*) have 8 trees each. — L & C: to 300 trees 3″ +, in 75 spp., on 1235.5 mlc.

MUJUKA: PLOT VI (PP. 21-23). In another large tract of Urwald s. of Hauptlingsdorf Mujuka, near km. 59. On level, porous, lateritic soil. Structure of virgin forest, with fewer small trees and high proportion of very large trees. One Njabibaum (*Mimusops djave*) was 207 cm. in diam., 68 m. high, volume 137 cu. m. Jentsch points out that for forest with so many large trees, a half-hectare plot is too small. 182 trees 7 cm. +, in 52 spp. — L & C: to 170 trees 3″ +, in 49 spp. on 1235.5 mlc. Comparatively low density.

BEKILI: PLOT III (P. 21). Within the cultivated district of the Mukonje plantation, in an area cut by ravines and always forest-covered. A several-storied primary stand. 293 trees 7 cm. +, 67 spp. L & C: to 268 trees 3″ +, 62 spp., on 1235.5 mlc.

SONG-BO: PLOT X, AND EDEA: PLOT VII (PP. 23-25). Tallies for these plots are so nearly the same as for Plot III that separate curves for them were not drawn. No. X is 2 days journey s. w. of Ngongnkeng near Song-bo village, 1 km. e. at ca. 250 m. elev. Level ground with Urwald. Laterite developed from gneiss. The plot included 7 trunks of Bokokólo, abundant nearby, some of giant size, with enormous knobby stems up to 5 m. diam. 292 trees 7 cm. +, 67 spp.; to 273 trees 3″ +, 65 spp. Likely value for Am: 5100 mlc., with 92 spp. Trees per acre, 221 (3″ +).

Plot VII is in the untouched primary forest n. of Edea. Level to gently east-sloping; stony to gravelly lateritic loam. No giant trees present. Under the largest trees *Lophira alata* is dominant. 8 or more other spp. are notable. 280 trees 7 cm. +, 66 spp.; to 264 trees 3″ +, 63 spp. Likely value for Am: 5140 mlc, with 90 spp. Trees per acre, 214.

MANOKA: PLOT XII (P. 27). On the densely forested Manoka peninsula. Level ground, sand with humus. Old-growth forest, from which some middle-sized trees have been cut. The large dominant trees of *Lophira alata* remain [1909]. Notably poor in spp. 184 trees 7 cm. +, 19 spp.; in slightly larger plot, .51 ha. — L & C: to 172 trees 3″ +, 18 spp., in 1260 mlc. Lowest density among Jentsch's plots.

SECONDARY FORESTS, KAMERUN. JENTSCH (1911). Four of Jentsch's plots are in cut-over stands. One of them, No. IX at Ngongnkeng (pp. 16, 24-25), was not used for a species-area curve, since its canopy is an even-aged pure stand of Schirmbaum, *Musanga Smithii*, an opportunist species of openings and

clearings. If data were available for the understory (a mixture of many species), or for the canopy that may have developed since Jentsch's observations in 1909, the usual type of S-curve might be expected. Plots I and IV were in the same districts as Jentsch's old-growth Plots II and III.

NJABI: PLOT XI (P. 26). On left bank of lower Sanaga River, ca. 4 km. s. w. of Njabi village, in a long-settled district which is a mosaic of cultivated areas and of young, middle-aged, and old forests, mostly secondary. The plot is at ca. 50 m. elev., is level, in laterite with clayey subsoil. The stand is mostly of small trees, with oil-palms, weedy herbs, and many climbers. It is representative of an area 15 × 100 km. Njabi trees, *Mimusops djave,* are frequent to abundant over this area. 369 trees 7 cm. +, 147 spp., on .5 ha.—L & C: to 337 trees 3″ +, 135 spp., on 1235.5 mlc. Fairly high density added to inherently profuse mixture of species gives this stand the greatest number of species at minimum area (Sm = 203) and at one acre (129) among all the forests studied. Jentsch's primary stand on Plot VIII is second to this one.

JOHANN-ALBRECHTS HÖHE: PLOT I (P. 18). Location 2 km. w. of Kumba village on road to Buea. Ca. 245 m. elev. Lateritic loam on yellowish subsoil; level surface. An earlier stand was long ago removed by the natives, except for a few giant trees. Most trees (89.5%) are in the 7-20-cm. class. Weedy climbers are abundant. Two-story mixture, with ca. 11 top-story trees per hectare. 323 trees 7 cm. +, 111 spp., on slightly larger plot, .54 ha. — L & C: to 292 trees 3″ +, 104 spp., on 1334 mlc.

BEKILI: PLOT IV (P. 18). Near the Mukonje Plantation at ca. 150 m. elev., in level area. This a younger stand than on Plot I. It includes oil-palms scattered and in groups, weedy tall herbs, and climbers. 227 trees 7 cm. +, 60 spp., on .5 ha.—L & C: to 209 trees 3″ +, 58 spp., on 1235.5 mlc.

LIKOMBA FOREST, NEAR KAMERUN MOUNTAINS. CA. 50 M. ELEV. J. MILD-BRAED (1930A, 1930B). An extensive tract, 14 × 3 km., flat over wide stretches. Mildbraed enumerated trees 30 cm. d.b.h. and larger, in each of 15 1-hectare Probeflächen. From 30 cm. to 7.62 is too large an interval for safe extrapolation, therefore data have been used for only one plot, No. VII, for which maps of 2 parts, each .4 ha., are given (1930b: 955-956), with complete listing of trees and species. On 1 ha., 9 spp. exceed 60-cm. diam. 6 spp. lead: *Pterygota macrocarpa, Lophira procera, Terminalia superba, Hylodendron gabunense, Alstonia congensis, Homalium africanum,* with possibly 2 others. Given: 81 ? trees 30 cm. +, in 27 ? spp., on 1 ha.; and 35.5 trees 30 cm. +, in 16 spp., on .4 ha. Conversion, L & C: to 270? trees 3″ +, in 33.9? spp. on 2471 mlc.; and 104? trees 3″ +, in 26.3? spp., on 988 mlc. Mildbraed states that this forest is floristically poor in comparison with Jentsch's and with some others he had seen. At minimum area, Likomba Plot VII is somewhat richer than Jentsch's Manoka Plot (39.3 to 36.4 spp.). At one acre it is far richer than Manoka (26.4 to 16.7).

Of Mildbraed's 14 other plots, only one, Likomba XII, has as many trees (30 cm. +) as VII. In XII, also in V, the no. of spp. represented by trees of this size is slightly greater than in VII. In the whole 4200 ha. of the Likomba tract he suggests a minimum of 300 woody spp. (A possible maximum is 430.)

TROPICAL FORESTS: SOUTH AMERICA

TABLE 7. Tropical Forests: South America.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Moraballi Creek, British Guiana						
Greenheart forest	8 440	34 156	76.1	114.4	246.9	3
Mixed rain-forest	8 550	34 601	79.2	118.9	203.9	2
Wallaba forest	10 000	40 469	64.1	96.1	285.9	3
Morabukea forest	19 500	78 914	70.2	103.5	143.1	3
Mora forest	21 650	87 615	68.2	100.7	141.0	3
French Guiana: Tollinche	10 070	40 752	58.6	85.7	130.7	3+
Camp Godebert	11 724	47 446	78.8	115.5	165.0	3+
Oyapock	18 050	73 046	98.0	141.5	148.7	3+
Eastern Brazil: Pernambuco	3 045?	12 323?	29.6	43.8	200?	3+
Southeastern Brazil: Lagoa Santa	3 475?	14 063?	58.8	87.8	200?	3+

TROPICAL FOREST, MORABALLI DISTRICT, BRITISH GUIANA. T. A. W. DAVIS AND P. W. RICHARDS (1933, 1934). Forests of 5 different sites. Main plots are 400 × 400 ft., with trees 4″ + given in tables; also trees <4″ and >15 ft. height in 2 strips each 25 × 400 ft.

GREENHEART FOREST, S. P. 4 (SAMPLE PLOT 4, IN TABLE 5, P. 150; P. 119). The type is confined to porous reddish-brown sand, chiefly on ridge-slopes. *Ocotea Rodioei* forms 43.4% of trees 16″ +. *Pentaclethra macroloba, Eschweilera Sagotiana,* and *Licania venosa* are also abundant. Ca. 91 other tall-tree spp. Since greenheart areas are narrow, the table is for 2 plots, together equaling 160,000 sq. ft. On these, 773 trees 4″ +, in 94 spp. On the 2 25-ft. strips, 325 trees 15 ft. high +. Conversions L, C, and I: to 907 trees 3″ +, in 97 spp., in square plot of 3672 mlc. Also, 113 trees 3″ +, in 40 spp., in square of 459 mlc.

MIXED RAIN-FOREST, S. P. 3 (PP. 142-146; ALSO TABLES 1 & 2). This type covers much of the lower hilly lands, usually in rather sticky yellow-brown loam. *Pentaclethra macroloba, Licania* (3 spp.), *Eschweilera* (4 spp.), and greenheart, are leading spp. Ca. 85 other tall-tree spp. 644 trees 4″ +, in 90 spp., on main plot. On clear-felling strips 200 × 25 ft., 102 and 106 trees 15 ft. ht. +, in 36 and 39 spp. On strip 400 × 25 ft., 57 trees 40 ft. ht. + in 25 spp. — L, C, & I: to 749 trees 3″ + in 101 spp. on 3672 mlc.; 26 and 27 trees 3″ + in 16 and 17 spp., on 2 squares each of 114.8 mlc.; 43 trees 3″ + in 19 spp., on square of 229.5 mlc.

WALLABA OR WHITE-SAND FOREST. S. P. 5 (PP. 122-126, TABLE 6). This most distinctive type, dominated by *Eperua falcata,* occupies white sand of high

hill ridges. Density is fairly high, a consequence of inferior site; buttresses are almost completely absent; canopy is fairly open, with less constantly humid air. *Catostemma fragrans* and *Licania buxifolia* are subdominant. *Cassia pterido-phylla, Eperua Jenmani,* and *E. grandiflora* are also abundant. 919 trees 4″ + in 70 spp., on main plot. 399 trees 15 ft. ht. + on the 2 strips each 25 × 400 ft. — L, C, & I: to 1050 trees 3″ + in 77 spp., on 3672 mlc. 131 trees 3″ + in 33 spp. on square of 459 mlc.

MORABUKEA FOREST S. P. 2 (PP. 113-116, TABLE 3). Dominant species is *Mora Gonggrijpii.* The forest is dense, with heavy shade, commonly on lower slopes of smaller hills, and occupies much of the total area. Soil is heavy red clay, probably lateritic, finer than ·that of mixed type. Subdominants are *Eschweilera Sagotiana, Catostemma commune, Pentaclethra macroloba, Ocotea Rodioei, Licania venosa.* 460 trees 4″ + in 70 spp., on main plot. 176 trees 15 ft. ht. + on the 2 25-ft. strips. — L, C, & I: to 526 trees 3″ + in 69 spp. on 3672 mlc.; 66 trees 3″ + in 25 spp., on square of 459 mlc.

MORA FOREST, S. P. 1 (PP. 106-113, TABLE 2). The dominant *Mora excelsa,* larger and with higher buttresses than morabukea, occupies lowest ground, in strips along river-banks and creeks. These are flooded for considerable periods. Soil is usually moist through dry season. The type occurs also in shallow soil of some rocky slopes. Subdominant are *Pterocarpus officinalis* (corkwood), *Pen-taclethra, Aldina insignis. Eperua Schomburgkiana* & *Macrolobium bifolium* are characteristic species. 462 trees 4″ + in 59 spp. on main plot; 154 trees 15 ft. ht. + on strips. — L, C, & I: to 518 trees 3″ + in 64 spp. on 3672 mlc.; 65 trees 3″ + in 23 spp. on square of 459 mlc.

TROPICAL FOREST, FRENCH GUIANA. A. BERTIN (1920). The valuable report by Bertin appeared at first to be unusable, since his 40-cm. diam. limit requires so radical an extrapolation in converting to 3-inch limit. Conversion was tried experimentally by three methods, using stand-graph and cumulative stand-graph made from Bertin's Table 3, and the cumulative graph for Brownfield Woods. The ratios found for number of trees 3″ + to number of trees 40 cm. (15.75″) + are: 3.26 or higher, 3.78 or higher, 5.64. These ratios give from Bertin's 2676 trees 40 cm. + on 34 hectares the following numbers of trees per acre: 103.8 or more, 120.3 or more, 179.6. If one adopts as a likely estimate of density, 165 trees per acre, the total for Bertin's 34 ha. becomes 13,860 trees 3″ +. The ratio of this number to his 2676 is 5.181. This multiplier makes possible a prob-ably fair comparison of Bertin's forests with others. Its application to 3 of his districts follows.—These treatments of Bertin's forests and of two Brazilian ex-amples should be regarded as speculations more than as computations. They are accordingly assigned in Table 7, a dependability rating of 3+ rather than 3. These forests are not used in summarizing data for tropical forests in general.

TOLLINCHE AND CRIQUE SPAROUINE DISTRICT, MARONI (PP. 16-17, TABLE 4). The species with the most very large trees is *Caryocar glabrum:* most

abundant are *Dicorynia paraensis,* Bois grage blanc, Simarouba, Goupi rouge franc (*Goupia* sp.), Grignon franc, and Maho cigare. The total is 934 trees 40 cm. + in 75 spp. on 15 ha. In Table 8 (pp. 29-32), a 1-ha. parcelle has 74 trees 40 cm. + in 27 spp. — Conversion for 15 ha., L (multiplier 5.181) & C: to 4841 trees 3″ + in 104.5 spp., on 37.07 acres. The 15 ha. is probably a composite.

DISTRICT OF CAMP GODEBERT AND CRIQUE ACCAROUANY, MARONI (PP. 13-15, TABLE 3). *Eperua falcata, Dicorynia, Ecclinusa sanguinolenta, Licania galibica,* and *Manilkara balata* are most numerous. The 34 ha. probably is a composite of separated areas representing several types. 2676 trees 40 cm. + in 118 spp., on 34 ha. A 1-ha. parcelle has 86 trees 40 cm. + in ca. 18 spp. Conversion for 34 ha., L & C: to 13,860 trees 3″ + in 152? spp., in 84 acres.

DISTRICT OF OYAPOCK (CRIQUE BALATÉ AND ENVIRONS DE ST. GEORGES) (PP. 21-23, TABLE 6). *Goupia glabra, Dicorynia, Eperua, Manilkara, Licania,* and *Ecclinusa* are commonest. The 9-ha. sample, probably a composite, has 638 trees 40 cm. + in 98 spp. These convert to 3307 trees 3″ + in 147? spp., on 22.23 acres. There is also a 1-ha. parcelle with 58 trees 40 cm. + in 25 spp.

It is probable that the reference areas for Bertin's prospections are larger than would be the case if each represented a single forest type. For such a type the reference areas would perhaps be .5 to .7 of the size found for one of the three sets of data here treated.

NO PLOT DATA FOR AMAZONIA are known to the writer. F. F. NETTO (1945: 38) says: "In the entire Amazon Valley the flora is so intermixed that if a sq. km. of ground could be marked off only a single specimen of any one of the different kinds of trees probably might be found therein. Nevertheless, zones do exist where a single or sometimes a group of species occur in denser stands. For example, the oil palms are numerous in the region of the Islands; Brazil nut in the Middle and Upper Tocantins River; and "jarina" [ivory-palm] in the Middle Solimões. A further exception must be made for the "guaraná," which is found only in the municipality of Maués and vicinity, in the State of Amazonas. For the others dispersion is the rule . . . ."

PERNAMBUCO FOREST, EASTERN BRAZIL. V. SOBRINHO (1937). The original report was not accessible; in the abstract by B. E. DAHLGREN one finds that the forest is old-growth, with all age-classes, and composed of both hard and soft timbers. Low vegetation in the area studied had been cleared out by fire. A burnt area of 5000 sq. m. was studied; 704 trees of unspecified diam.-limit represent 49 spp. Av. interval between trees is 7 m. (est.). The mixture must be thorough, since the 3 commonest trees, *Carapa* sp., *Heliotropium* sp., and *Protium* sp. occur in small numbers: 35, 31 and 27 (93 of the 704). Conversion to 3″ limit is impossible with no more information as to size of trees. The enumeration presumably includes saplings and arbuscules; with the more sizable

trees also, density as given is 569 per acre. If one assumes that on the basis used for other forests, this one is moderately dense, a likely number per acre (based on 3″ diam.-limit) is 200. On this assumption, C-conversion gives 34.7 spp. for 200 trees, 22.2 spp. for 60 trees, 12.1 spp. for 20 trees, on 1000, 300, and 100 mlc. From these figures a tentative species-area curve was made, and from it tentative reference areas computed.

LAGOA SANTA, SOUTHEASTERN BRAZIL. E. WARMING (1899). A much-cited but not very explicit statement of tropical *richesse florale*. Where Warming could study trees as they were being cut down, he found, in 6 different cases, that 50-250 trees represent 27-91 spp. It was thought interesting to treat this example in the manner of the preceding, using the same assumption of 200 trees 3″ + per acre. The median number of trees, 150, was found by C-conversion to represent 45.4-73 spp.; mean is 59.2. If the sizes included by Warming are the same as those listed by Sobrinho, 150 such trees occupy 263.7 mlc. The number of trees 3″ + which occupy this area is 52.74. C-conversion suggests 34.7 spp. for 52.74 trees. For 200, 50, and 20 trees, species-numbers are 66.7, 37.5, and 16.7, on 1000, 300, and 100 mlc. As thus computed, floristic richness is above average, but not exceptional.

SUBTROPICAL THICKET AND HEATH, MAURITIUS

	Am, *mlc.*	Am, *sq. m.*	S_1	Sm	N1000	D
Sideroxylon thicket	92.4	374	44.8	69.0	15 520	1
Philippia heath	163.9	663	18.4	28.0	8 920	1

SIDEROXYLON THICKET, MAURITIUS. R. E. VAUGHAN & P. O. WIEHE (1941: 150). This thicket is an early stage of mixed forest, and is placed with shrub vegetation rather than forest because the size and spacing of plants, and sizes of reference areas, are closer to shrub types than to forest. Two dominant species, *S. Bojerianum* and *S. puberulum,* form open canopy 8-10 m. high. Under it is a dense closed stratum with ca. 80 spp., and 3500 individuals 50 cm. ht. + in 1000 sq. m. Beneath this are herbs and small shrubs. More abundant species are *Eugenia orbiculata, Securinega durissima, Erythrospermum mauritianum, Antirrhoea verticillata, Aphloia theiformis, Erythroxylon laurifolium.* Vaughan and Wiehe give species-area curves drawn to linear coordinates.

PHILIPPIA HEATH, MAURITIUS. VAUGHAN & WIEHE (1941: 148). The term heath is appropriate, since *Philippia* is in *Ericaceae.* This shrub formerly covered large areas. It is adapted to unweathered lava exposed to violent rains and to long periods of tropical sun. Three species peculiar to it are dominant: *Philippia abietina, Phylica mauritiana, Helichrysum yuccifolium. Aphloia theiformis* is next abundant after *Philippia.* The semi-open shrub stratum is 1-3 m. high. Under it are *Gleichenia, Lycopodium,* and *Cladonia.* The authors give species-area data for 9 plot-sizes, from 4 spp. in 4 sq. m. to 30 spp. in 1000 sq. m. The size-limit is presumably 1 cm. diam. or 50 cm. height.

CHAPARRAL AND BUSH, CALIFORNIA

For much of the data on chaparral, the writer is indebted to the California Forest and Range Experiment Station. By chaparral is meant the evergreen shrub of fairly high rainfall belts of California foothills and mountains, in which species of *Adenostoma, Ceanothus, Arctostaphylos,* or *Quercus* usually dominate. By *California bush* is meant a highly variable complex of bush communities. (Bushes have many small, short-lived, not-very-woody stems, in contrast with the fewer, thicker, woodier, and longer-lived stems of most true shrubs.) California bush is more inclusive than the several associations comprising the coastal sagebrush formation or climax of Clements. *Artemisia californica* and bush species of *Salvia, Eriogonum, Lupinus, Eriodictyon, Diplacus,* and *Aplopappus* are among the notable plants. Their leaves are commonly specialized in various ways, many being resinous, strongly aromatic, heavily tomentose, revolute, or linear. As compared with chaparral, bush commonly occurs in low-rainfall zones or in drier sites, in finer soil or on less steep and rocky slopes, or at lower elevations, or in more recently disturbed areas. In places it forms a narrow border or a broad zone between chaparral and grassland. At least some bush types and most forms of chaparral are well adapted to fire and prevail where fires are recurrent. Some species are members of both formations. The type designated by J. S. Horton as chamise-sage is intermediate.

In some chaparral and bush areas it is impracticable to distinguish and thus to tally plant individuals. The numbers per acre given in four instances in Table 8 are very rough estimates.

TABLE 8. Chaparral and Bush, California.

Stand or type	Am. mlc.	Am. sq. m.	Sr	Sm	N1000	D
Mixed chaparral, Bell Canyon	88.6	359	13.5	19.7		3
Oak chaparral, Bell Canyon	79.0	320	13.5	19.7		3
Oak chaparral, Tanbark	262.1	1061	15.0	22.6		1
Chamise type, Bell Canyon	87.8	355	11.7	17.0		3
Chamise type, Tanbark	186.2	753	12.0	17.9		2
Chamise type, San Rafael Hills	450.0	1820	9.9	14.6	2570?	1
Chamise-sage, Bell Canyon	56.5	229	8.7	12.6		3
Chamise-sage, base of Mt. Lowe	273.8	1108	13.2	19.5	3860?	1
Mixed bush, Verdugo & S. R. Hills	136.1	551	9.3	13.8	4500?	2
Bush near Mt. Lowe	134.3	543	6.9	10.2	6520?	1

MIXED CHAPARRAL, BELL CANYON, SAN GABRIEL MOUNTAINS. J. S. HORTON (1941: 461-463). Bell Canyon is tributary to Big Dalton Canyon, which opens at the steep south front of the San Gabriel Mts. between Glendora and San Dimas. In four small watersheds (catchment areas) forming the amphitheater-like head of Bell Canyon, 222 1-milacre plots were established near horizontal trails at four levels, 2550 to 3300 feet, and spaced at 132 ft. intervals. These plots are in four chaparral types, only 20 representing the mixed type. 20 species

of woody plants, not all of the size and growth-form characteristic of chaparral dominants, are represented in the plots. Average number of species per plot, readily found from Horton's frequency tables on pp. 462-463, is 4.10. 40.2% of the ground surface is bare. *Ceanothus crassifolius, Photinia arbutifolia,* and *Arctostaphylos glandulosa* are dominant, making 50% of the plant cover. 9 other species contribute much to the bulk of the vegetation, among them *Adenostoma fasciculata* (chamise), *Salvia mellifera* (black sage, a bush), and *Garrya Veatchii.* I-conversion from aggregate area of 20 separated plots gives a one-piece equivalent area of about 96 milacres. Thus for this and 3 other types in Bell Canyon, 2 points for a species-area curve are available.

Horton has since studied this same type at higher elevations. He now designates it broad-leaved chaparral, principally because the needle-leaved chamise is absent or infrequent. *Q. dumosa* is also insignificant in broad-leaved chaparral; and in locations other than Bell Canyon *C. crassifolius* is unimportant.

A somewhat different chaparral mixture on a northeast slope at Stough Park at ca. 1500 ft. elev. in the middle part of the s. w. side of Verdugo Hills, observed in 1944, has 17 spp. in 1 acre. *Quercus dumosa* is abundant. In addition to some of the Bell Canyon spp., *Rhus integrifolia, R. laurina,* and the thicket-forming semi-woody grass *Elymus condensatus* are present.

OAK CHAPARRAL, BELL CANYON. HORTON (1941: 461-463). 33 of the 222 plots are dominated by *Quercus dumosa, Ceanothus crassifolius,* and *C. oliganthus,* making over half of the cover. *Salvia, Cercocarpus betulaefolius, Photinia, Prunus ilicifolia,* and 3 other species are important. The oak shrubs are broader and taller than others. Oak chaparral and mixed chaparral are the least xeric types of the district. The average 1-milacre plot has 4.94 spp. Aggregate species-number is 22. One-piece equiv. area is 150 mlc.

OAK CHAPARRAL, TANBARK EROSION PLOTS. DATA BY CALIF. F. & R. E. S. The location is near Tanbark Flat, elev. ca. 2750 ft., in north fork of San Dimas Canyon. Slope is to the east, ca. 33%. Soil is deep, with no exposed rock. It is a less xeric exposure than Bell Canyon. The plots are in down-slope strips, each 10 × 110 ft., in contiguous groups of 3, with 3 such groups close together (strips 321-329). Strip 321 is of a different type. Strips 323-329 form the present sample of oak chaparral. Original data were studied at the Glendora office, and average species-number per plot was determined for each of 22 sizes, from 2.44 spp. at 100 sq. ft. (2.295 mlc.) to 21.0 spp. at 172.8 mlc. The same 3 species dominate as in Bell Canyon. *Salvia* is absent, *Cercocarpus* is locally abundant, and *Penstemon cordifolius* is locally frequent. *Arctostaphylos glandulosa* is replaced by *A. glauca.* — Fig. 2 (p. 5) is the S-curve for this oak chaparral.

CHAMISE TYPE, BELL CANYON. HORTON (1941: 461-463). This is the extensive type, occupying 147 of the 222 plots. *Adenostoma* and *C. crassifolius*

dominate; *Salvia mellifera, Eriogonum fasciculatum,* and *Q. dumosa* are the 3 other leading species. 51.8% of the ground surface is bare. Spp. per 1-mlc. plot, 3.52. Aggregate species-number is 22. One-piece equiv. area is 500 mlc.

CHAMISE TYPE, TANBARK PLOTS. DATA BY CALIF. F. & R. E. S. One strip 10 × 110 ft., No. 321 of the 9 strips mentioned with oak chaparral. Between strips 321 and 323 is a change in direction of slope, giving more xeric exposure to No. 321. From original plot-maps and records at the Glendora office, species-numbers for 6 plot-sizes were found, from 2.91 at 2.295 mlc. to 10.0 at 22.95 mlc.

CHAMISE TYPE, SAN RAFAEL HILLS. A. G. VESTAL, AUGUST, 1944. These and the Verdugo Hills form an outlier of the San Gabriel Range near its southwest base. They are separated from the range by an alluvium-filled pass 10 miles long, and 1 mile or more wide, trending northwest-southeast, in which lies a line of towns from Sunland to Flintridge. The smaller, more easterly San Rafael Hills are separated from the more massive Verdugo Hills by Verdugo Canyon. The area studied is at ca. 1200 ft. elev. near the southeast extremity of San Rafael Hills. It comprises 12 contiguous plots 20 ft. square, plus an adjacent area equal to 12 plots. Analysis provided species-numbers for 6 sizes, from 4.75 at 9.18 mlc. to 13.0 at 220.3 mlc. *Adenostoma* is dominant. *Salvia mellifera* and *Eriogonum fasciculatum* are abundant enough to bring this stand close to the chamise-sage type. *Cercocarpus* and *Yucca Whipplei* are moderately frequent.

CHAMISE-SAGE TYPE, BELL CANYON, HORTON (1941: 461-463). This xeric type occupies 22 of the 222 Bell Canyon plots. 76.1% of the surface is bare. *Eriogonum, Adenostoma,* and *S. mellifera* dominate. Other leading species are *C. crassifolius, Eriodictyon trichocalyx,* and *S. apiana.* Spp. per plot, 3.10. Spp. in 22 plots, 14. Equiv. one-piece area, 105 mlc.

CHAMISE-SAGE, BASE OF MT. LOWE. VESTAL, AUGUST, 1944. Xeric slope at ca. 1800 ft. elev., southwest part of San Gabriel range at Altadena. The area had been burned a few years earlier. Dead stems were still evident. Dominant shrubs of *Adenostoma* were 2.5-5 ft. high. *S. apiana, Artemisia californica,* and *Eriogonum* are the principal bush species. 20 6-mlc. plots, + 2 18-mlc. plots were listed. 6-mlc. plots are 19.23 × 13.59 ft., a size convenient for shrub vegetation. Analysis gave species-numbers for 10 plot-sizes, from 6.0 spp. at 6 mlc. to 19 spp. at 240 mlc.

A chamise-sage area at 1500 ft. elev. on a northwest slope near the northwest end of San Rafael Hills close to Montrose, has 13 spp. in ca. 400 mlc. Another chamise-sage south slope at Stough Park at ca. 1500 ft. elev., in the Verdugo Hills, above Burbank, has 15 spp. in a 400 mlc. sample.

MIXED BUSH, VERDUGO AND SAN RAFAEL HILLS. VESTAL, AUGUST, 1944. The curve for moderately to highly mixed bush is a composite for four stations

within a few miles of one another. One is an area of disturbed bush near south-east end of San Rafael Hills, with 19 spp. in 3 acres. *Artemisia, Eriogonum, Lotus scoparius, Senecio Douglasii, Salvia mellifera* are notable. Also present are *Adenostoma* and a few other shrubs, probably survivors from former chaparral. — No. 2 is an alluvial flat sloping slightly southwest at base of north-west end of San Rafael Hills, just s. of Montrose. It is below hills with chamise-sage cover, and receives an infusion of shrub species therefrom. Parts of this flat are disturbed with thinned and weedy bush. It has 22 spp. in 6 acres. *Artemisia, Eriogonum, Salvia apiana, Aplopappus (Ericameria) Parishii, Rhamnus crocea* var. *ilicifolia, Senecio,* are the common species; *Tetradymia comosa* and *Lonicera subspicata* are conspicuous. — No. 3 is the flat, open, disturbed lower part of Sunset Canyon in Verdugo Hills above Burbank. It has 18 spp. in 2 or 3 acres. — No. 4, in many ways notable, is an alluvial flat between low mountain spurs at Stough Park, higher in a branch of Sunset Canyon. It is 100-200 ft. wide, 1800 ft. long. It is slightly trenched by recent erosion. Chaparral covers the adjoining spur ridges. The flat has rather rich bush cover, also with infusion of chaparral shrubs, making 25 spp. in 8.3 acres. Among species not in the other 3 stations are *Rhus integrifolia, R. trilobata, Diplacus longiflorus,* and *Aplopappus (Ericameria) pinifolius.* In moderately mixed bush, as the curve for this composite suggests, one may expect 13 spp. in 0.1 acre, 18 spp. in 1 acre, and 22.4 spp. in 10 acres.

BUSH, NEAR BASE OF MT. LOWE. VESTAL, AUGUST, 1944. This bush occupies the head of an alluvial fan, below the steep basal slope of the San Gabriel Range, near Altadena. *Artemisia* and *Eriogonum* are the dominants. *S. apiana* is locally abundant. *Lotus scoparius* occurs in interspaces among the larger bushes. 20 3-mlc. plots, and 10 6-mlc. plots, all contiguous, with 3 larger areas (one including the plots), make up the sample. The 3 larger areas are each ca. 878 mlc. There are 14, 13, and 12 spp. in these 3 areas, only 15 in all. Species-numbers for 14 plot-sizes were obtained, beginning with 4.4 for 3 mlc. and 5.35 for 6 mlc. Reference areas are larger than might be expected. This is attributed to the nearly complete domination by two species, leaving little room for individuals of others.

MEDITERRANEAN SHRUB VEGETATION

Two sources of plot data for maquis and garigue have been used for curves, samples being very small in all of the 7 localities. The resulting reference areas are markedly smaller than those found for chaparral and bush in California. It can not yet be said that this difference is real.

QUERCUS PUBESCENS–SPARTIUM–CISTUS. MONTE GAURO, NEAR NAPLES. 200 M. ELEV. J. Y. BERGEN (1903). Bergen's Plot E is described as open thicket on an east slope. The oaks are dominant, and grow to 3.5 m. high. 32 of them occur on a plot 10×10 m. *Spartium junceum* (22 indivs.), *Crataegus* (11),

TABLE 9. Mediterranean Evergreen Shrub and Bush.

Stand or type	Am, mlc.	Am, sq. m.	Sr	Sm	N1000	D
Quercus pubescens, Monte Gauro	27.67	111.9	5.53	7.13	5 704	3
Arbutus–Q. coccifera, n.e. Spain	6.64	26.9	7.52	11.07		3
Arbutus–Pistacia, etc., Capri	8.00	32.4	6.91	10.08	70 060	3
Erica multiflora, etc., s. France	6.65	26.9	10.77	15.76		3
Myrtus, etc., Pozzuoli, Solfatara Hill	6.50	26.3	5.61	8.18	59 060	3
Spartium–Cistus, etc. Capri, n.w. slope	10.00	40.5	5.34	7.74	29 610	3
Thymus, etc., near Lerida, n.e. Spain	6.70	27.1	4.91	7.10		3

Cistus salviaefolius (62), 3 other shrubs (14). 141 plants in 7 spp. on 24.71 mlc. For this and 3 other of Bergen's plots likely species-numbers for smaller areas were found from species-individuals curves (C-conversion). It is possible that Bergen counted each stem or shoot as a plant individual.

ARBUTUS–Q. COCCIFERA: MOUNTAIN MAQUIS AT TOP OF TIBIDABO NEAR BARCELONA, N. E. SPAIN. C. RAUNKIAER (1916: 235, TABLE 4). In order of frequency in 50 separated plots, each 0.1 sq. m. (est. effective plot-size 0.5 sq. m.): *Arbutus unedo, Q. coccifera, C. salviaefolius, Erica arborea, Calycotome spinosa,* and 7 other spp. incl. *Pistacia, Q. ilex, Q. pubescens.* Spp. per plot, 3.24. One-piece equiv. area, 10.69 mlc., with 12 spp. Two points available for a curve for this and Raunkiaer's other localities.

ARBUTUS–PISTACIA–QUERCUS–ERICA. CAPRI, FOOT OF MT. SOLARO, 130 M. ELEV. BERGEN (1903). Plot B is a close, dense thicket, 1 to 2.5 m. high. 1732 plants on 100 sq. m. *Arbutus* (464 indivs.), *Pistacia lentiscus* (44), *Q. ilex* (12), *Q. aegilops* (12), *Erica arborea* (12), *Rhamnus alaternus* (12), *Myrtus communis* (124), *Coronilla emerus* (812), *Smilax aspera* (200). 12 spp. on 24.71 mlc.

ERICA MULTIFLORA–GENISTA–ROSMARINUS: SOUTHERN FRANCE. RAUNKIAER (1916: 234, TABLE 3). Raunkiaer designates this, *Erica multiflora* formation. The results in Table 9 are for the bush phase of this vegetation, which includes also a grassland phase. A description, and results for the grass phase and for the vegetation as a whole, will be found in the later section on vegetation-complexes.

MYRTUS, ETC. POZZUOLI, SOLFATARA HILL, S. E. SLOPE, 120 M. ELEV. BERGEN (1903). 1460 plants in 10 spp. on 100 sq. m. *M. communis* (1000 ± 200 indivs.), *Cistus salviaefolius* (190), *Calycotome* (143), *E. arborea* (42), *Spartium* (33), *Q. pubescens* (13), *Q. ilex* var. (10). This is Bergen's Plot C.

SPARTIUM–CISTUS, ETC. CAPRI, N. W. SLOPE, 350 M. ELEV. BERGEN (1903). Plot A, 100 sq. m., 732 plants of 9 spp. *S. junceum* (106), *Cistus villosus* and *C. salviaefolius* (603), *Myrtus* (15), *Daphne Gnidium* (4), *Pistacia, E. arborea, Olea europea,* and *Q. pubescens* (1 each). Near, but not in plot:

Cytisus spinescens ramosissimus, Euphorbia spinosa, Satureia montana, Pinus halepensis.

On Monte Gauro, w. slope, ca. 190 m. elev., Bergen described Plot D with only 2 species, *Colutea arborescens* and *Spartium*. Near D in scanty soil, exposed to full sun, was Plot G, in a vegetation almost wholly composed of *Pistacia* and *Calycotome*. At a lower level was a considerable tract of saplings of *Castanea sativa*, with *Cytisus* (probably *C. scoparius*). These are like the simpler communities of chaparral or bush in California, in which one species, as *Adenostoma* or *Q. durata* or *Ceanothus cuneatus*, dominates, with only a few individuals per acre of any other shrub species.

THYMUS, ETC., 2 KM. E. OF LERIDA, N. E. SPAIN. RAUNKIAER (1916: 233). *T. hiemalis* seems to be strongly dominant, occurring in all 50 of Raunkiaer's plots, whereas none of the 6 other species occurs in more than 4. These include: *Teucrium polium, Helianthemum hirtum, Santolina chamaecyparissus,* and *Genista scorpius.* Effective plot-size for this *tomillar* is est. at .3 sq. m.; spp. per plot, 1.24; one-piece equiv. area 6.41 mlc. The reference areas are relatively large, for the same reason as with the bush near Mt. Lowe: nearly exclusive occupation by the dominant.

NORTH-EUROPEAN HEATH AND DWARF-SHRUB VEGETATION

The resemblance between west-Mediterranean shrub types, which include actual heaths, to the heaths and ericaceous dwarf-shrub communities of western and northern Europe, and the transitions to Arctic dwarf-shrub, have been pointed out by European plant geographers. The descriptions most readily available for the present treatment are those by Raunkiaer, Du Rietz, and Vahl.

Many species that are characteristic and dominant in these shrubby plant covers enter into the field-layer of open forests, and are components in some of the phytocenoses of North-European bogs. These species will again be encountered in the treatments of these vegetation-types.

TABLE 10. North-European Heath and Dwarf-Shrub.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Nackte *Calluna*, Insel Jungfrun	103.2	418	8.02	12.0	2
Calluna—Hylocomium Heide, Komosse ·	29.2	118	13.0	18.9	3
Calluna (no. 17) at Østerhede	22.0	89.0	2.50	3.66	3
Calluna—Arctostaphylos, Tinghede	28.5	115	9.88	14.3	3
Empetrum—Hylocomium, Torne Lappmark	61.7	250	11.0	15.9	2
Empetrum—Stereocaulon, Scand. Mts.	35.9	145	10.8	15.7	2
Dryas heath, Njulja, Lapland	21.3	86.3	11.7	16.9	3
Vaccinium—Dryas heath, Njulja	14.9	60.4	19.0	27.9	3

NACKTE-CALLUNA HEIDE, JUNGFRUN. G. E. DU RIETZ (1921: 158) "*Nackte*" describes the nearly bare ground surface (from scarcity of mosses

and lichens). It suggests poor site quality. This widely occurring heath type is of special importance in the Skärgarden or groups of rocky islands of south Sweden. No other plant approaches *Calluna vulgaris,* common heather or ling, in abundance. Other woody plants are *Vaccinium myrtillus, V. vitis-idaea;* dwarfed *Populus alba* and *Sorbus; Empetrum. Melampyrum pratense, Hieracium umbellatum,* and *Deschampsia flexuosa* occur in 38 down to 13 per cent of the quadrats. Species are listed for quadrats of 4 sizes, .01, 1, 4, and 16 sq. m. (effective plot-sizes est. as .03, .3, 1.06, and 4 mlc.). The numbers of quadrats of the 4 sizes are 1000, 100, 20, and 8. The plots are separated, are probably not confined to one stand, but all seem to be taken within a limited district in stands all of one rather closely defined type. 13 spp. in all occur in these plots. Spp. per plot: 1.06, 2.0, 2.5, 3.1. These species-numbers closely locate lower part of species-area curve; upper part is less dependable.

CALLUNA–HYLOCOMIUM HEIDE, KOMOSSE, SMÅLANDISCHE HOCHLAND. DU RIETZ, OSVALD, FRIES, AND TENGWALL (1920: 7). The rather rich ground layer of microphytes is not included in the species-count. 25 1-sq.-m. quadrats (effective size .3 mlc.) ; 7.72 spp. per plot; one-piece equivalent area 12.8 mlc., with 16 spp.

CALLUNA IN STERILE FLAT AT ØSTERHEDE, W. JUTLAND. RAUNKIAER (1910: 116, COLUMN 17 IN TABLE 36). 50 0.1-sq.-m. plots. *Calluna* in 50 plots, *Empetrum nigrum* in 6, *Carex panicea* in 18. No other species listed. Effective plot-size is est. at .4 sq. m , with 1.48 spp.; one-piece equiv. area, 8.58 mlc. Locality is between Lønborg and Lyhne. Very low and sparse ling vegetation.

CALLUNA–ARCTOSTAPHYLOS HEATH, TINGHEDE. RAUNKIAER (1910: 114-115, COLUMN 12 IN TABLE 35). "Højt Terraen vest for Tinghøjene paa Tinghede. Forunden Lyng og Rensdyrlav kun *Arctostaphylos* dominerende: *Calluna–Arctostaphylos* Facies." 11 spp. 2.48 spp. per plot. One-piece equiv. area, 8.58 mlc.

Raunkiaer gives on pp. 114-121 data for many heath types or variants. *Myrica, Erica, Calluna, Empetrum,* and *Arctostaphylos uva-ursi* are dominants in various combinations. The last 3 species dominate in localities summarized in columns 8 to 11 of Table 35, with *Calluna* in 48 to 50 plots in each. Numbers of spp. per plot in these 4 localities are 1.94, 2.16, 2.82, and 2.62. Totals of species listed: 5, 5, 8, and 6. No. 12 is therefore a heath rich in species; no. 17 is very poor in species.

EMPETRUM–HYLOCOMIUM TYPE, TORNE LAPPMARK. DU RIETZ (1921 : 159-160). *Empetrum* with ground layer rich in mosses is abundant in the Scandinavian mountains, and in the Skärgården. Du Rietz and his associates studied this heath on Mts. Luopahta and Nakerivaara. He lists the mosses and lichens on p. 159, but omits them from the field-layer species count (Table 13, p. 160). Plot-sizes are 1, 4, and 16 sq. m. In all of the large plots occur *Betula nana.*

Empetrum, Linnaea, Vaccinium vitis-idaea, and *Calamagrostis lapponica.* Other species of note: *Rubus chamaemorus, Salix glauca, V. uliginosum, Cornus suecica, Arctostaphylos alpina.* Spp. per plot in the 3 sizes: 8.01, 8.88, 9.50. Total spp., 17. Effective plot-sizes .3, 1.06, 4 mlc. Equiv. largest area, 95 mlc.

EMPETRUM–STEREOCAULON PASCHALE TYPE. DU RIETZ (1921:155, 157, TABLE 7). Predominant vegetation in continental mountain districts of northern Scandinavia. Du Rietz studied it in lower alpine zone of the same two mountains, which are on the south side of the eastern part of Torneträsk. 40 1-sq.-m. and 10 4-sq.-m. plots. 4.52 and 5.90 spp. per plot. Total spp. 14. Equiv. total area, 18.6 mlc. Most frequent spp.: *Empetrum, V. vitis-idaea, Betula, Calamagrostis, V. uliginosum.*

DRYAS HEATH, NJULJA, SWEDISH LAPLAND. M. VAHL (1913: 12-13; TABLE 7, COLUMN A). Vahl includes this type among "Formations above the limit of the birches." He describes 2 variants on the western declivity of Njulja above Björkliden. It occurs in deep raw humus. *Dryas octopetala, Salix reticulata, Cassiope tetragona, Arctostaphylos alpina,* and *V. uliginosum* are the common dwarf-shrubs. A few other plants are frequent. 50 0.1-sq.-m. plots, effective size .4 sq. m., with 5.28 spp. per plot. 14 spp. in all, on one-piece equiv. area est. at 8.58 mlc.

VACCINIUM–DRYAS HEATH WITH HERBS, NJULJA. VAHL (1913: 12-13; TABLE 7, COLUMN B). This has *V. vitis-idaea* in 43 of 50 plots, *V. uliginosum* in 42, *Empetrum* 32, *Cassiope* 23, *Dryas* 21. Herbs and grasses are numerous. Spp. per plot, 8.50; 25 spp. in all.

Du Rietz et al (1920: 7) give a summary of TENGWALL'S study of moss-rich *Dryas* heath at Nuolja. 54 spp. occur in 15 4-sq.-m. quadrats. Spp. per plot, 28.33. It is not stated whether the count includes mosses and lichens.

In reviewing the characteristics of these heath communities, including the figures of Table 10, one sees a wide range of variation in richness of composition. Very low site qualities with fewest species mark two of the *Calluna* stations. The opposite extreme is the herb-rich *Vaccinium–Dryas* community, which may be regarded as transitional between heath and grassland. Its reference areas are larger than those for most grasslands, smaller than for most heaths. Before much can be said about those communities which have only one to three species in the size of sample ordinarily studied, such as Raunkiaer's *Calluna* at Ø sterhede, additional field studies should be made. In this case the values for reference areas are very uncertain.

Although such impoverished types of vegetation can occur in any latitude with extreme exposure or poorest soil, it may not have been expected that notably rich heaths would be found above the Arctic Circle and at considerable altitude, as on Mt. Njulja.

SHRUB AND BUSH OF ROCKY MOUNTAINS
AND GREAT BASIN

The few types here treated make too fragmentary a sample of west-American shrub vegetation, but cannot well be included with any other group. Ramaley's descriptions of communities in the San Luis Valley of southern Colorado deal with types best represented in the Great Basin, but occurring elsewhere in the west.

TABLE 11. Shrub and Bush in Colorado.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Woody species, Boulder mesa	198.1	801	9.89	15.1	—	1
Sagebrush, San Luis Valley	44.7	181	3.56	5.30	3400	3
Chrysothamnus—Gutierrezia, V. G.	27.0	109	3.93	5.73	4673	3
Sarcobatus—Chrysothamnus, M.	19.2	77.7	2.00	3.17	798	2
Sarcobatus—Chrysothamnus, S. L. V.	46.0	186	2.60	3.78	2252	3

WOODY SPECIES IN MIXED VEGETATION OF ROCKY MESA-TOP ABOVE BOULDER. VESTAL, SEPTEMBER, 1944. This vegetation includes a very few stunted or young conifers scattered among shrubs and patches of inceptive grassland near the boulder-strewn edge of one of the high terraces flanking the outer mountain slope overlooking Boulder, Colorado. For description see the later section on mixed vegetation.

SAGEBRUSH, SAN LUIS VALLEY. F. RAMALEY (1942: 264, TABLE 8). This large intermont plain is in its northern part a basin with no exterior drainage. Its southwestern part is traversed by the Rio Grande. The bottom of the basin is mostly covered by greasewood. Sagebrush, and a more xeric bush–grass mixture of *Chrysothamnus, Gutierrezia,* and *Bouteloua,* occupy wide borders around the saline flats. *Artemisia tridentata* (At) dominates the finer-soiled, less xeric, areas. Its bushes are usually about 2 ft. high; each covers an estimated 7 sq. ft. on the average. With somewhat smaller plants of other species, one may expect to find about 3400 bushes per acre. Ground-space per bush is thus 0.294 mlc. Bushes cover a little more than half the surface. — At four different locations between Fort Garland and San Luis, Ramaley listed bush species in 50 0.1-sq.-m. plots. In all 200 plots, A. was represented by 136 bushes or clumps, *Gutierrezia diversifolia* or snakeweed (Gd) by 49, the first of several small-bush spp. of *Chrysothamnus* or rabbitbrush (C-1) by 18, and *Opuntia polyacantha* (Op) by 7 clumps. This enumeration determined proportions for leading species. Other bush or shrub species occurring with At may bring the woody-plant list to 15 or 16 species, but most are rare or local. Grasses of 4 or 5 species, and 3 dicot herbs (one is the Colorado rubber plant, *Hymenoxys floribunda*), are also listed in Ramaley's Table 8. — An incidental finding from his listing of bushes in such small plots as 0.1 sq. m. is that the effective plot-size may be 12.5 times the nominal size. Ramaley recorded on·200 plots,

210 bushes or clumps of the 4 woody species mentioned. If the 210 are of average size, each has the average ground-space of 0.294 milacres: the 210 represent aggregate ground-space of 61,78 mlc., $=$ 250 sq. m. Nominal area of 200 plots is 20 sq. m. Effective plot-size is 0.309 mlc. or 1.25 sq. m. — The one-piece area equivalent to an aggregate of 50 plots of this effective size was estimated to be 40.6 mlc. It includes 138 bushes.

To obtain species-numbers at particular areas, a result of an auxiliary study of tree distribution into plots was used. The object had been to find the "number of available individuals per plot" required to make it likely that a species will occur in a plot. If individuals were perfectly dispersed, a density of one plant for each two plots would give equal chances that the species would or would not occur in a particular plot. Since individuals are not so dispersed, the density which does give 50% probability of occurrence was found by observation for 4 tree species over a range of plot-sizes from that of Ar (smallest representative area, or 0.2 Am) down to $\frac{1}{64}$ Ar. For an irregularly distributed species, a density of 0.88 individuals per plot was found to give 50% probability of occurrence. Thus if a number of plots are of such size that the available population for each assures the presence of 4 species with possibility of a fifth, and with the fifth or least numerous species represented by 0.88 individuals per plot, then half the plots will have 4 species, the others will have 5: average species-number is 4.5. —Areas at which species-numbers are successively 7.5, 6.5, 5.5, . . . 2.5 were found by partly graphic, partly trial-and-error applications of the hollow-curve principle. The likely proportions for numbers of individuals of 4 minor species were found by extending a J-shaped curve determined by proportions for the 4 leading species. The population to go with a particular species-number was found by fixing the number for the least numerous species at 0.88 and proportioning numbers for other species to that one. Area for that population was found by means of the known ground-space per bush (0.294 mlc.). Results for all sizes of area are best shown in tabular form. Figures in the body of the table are numbers of individual bushes or clumps. The middle row of figures is the basis for all the others. — Incidentally, we see that for that row, i.e., for

TABLE 11a. Sagebrush: Populations and Areas at Particular Species-Numbers.

Species No. of spp.	At	Gd	C 1	Op	5th	6th	7th	8th	Population	Area, mlc.
7.5	3024	540.4	198.5	76	30	12	4	.88	3885.8	1142
6.5	332.7	119.0	43.7	16.7	6.6	2.7	.88		522.3	153.6
5.5	110.9	39.7	14.6	5.6	2.2	.88			173.9	51.2
4 +	89.5	32.0	11.75	4.5	?				137.75	40.6
4.5	44.4	15.9	5.8	2.3	.88				69.3	20.4
3.5	17.5	6.3	2.3	.88					27.0	8.0
2.5	6.7	2.4	.88						9.98	2.9

The species-area curve, based on figures in first and last columns, gives the Am-value 44.7 mlc. This is a little larger than the one-piece area equivalent to a set of 50 of Ramalev's plots.

the area equivalent to an average set of 50 small plots as observed by Ramaley, the number of bush species that he lists should be interpreted, not as "4," but as "between 4 and 5." The same degree of uncertainty usually applies to any species-number observed on a plot or tract.

Sagebrush in its extensive stands in the Great Basin and in mountain areas bordering it, has different associates, different sizes and spacings, and consequently different species-area relations, from those in the San Luis Valley.

CHRYSOTHAMNUS–GUTIERREZIA BUSH, SAN LUIS VALLEY. RAMALEY (1942: 260, TABLES 5-7). This is part of a bush–grass mixture treated in detail in the later section on mixed vegetation. Stands of this rabbitbrush–snakeweed type commonly adjoin areas of sagebrush and include mostly the same species. It is more xeric than sagebrush, is usually in coarser soil, has higher proportion of surface occupied by grasses and xeric herbs. There is likewise more bare soil, and the bushes are smaller and more widely spaced.

SARCOBATUS–CHRYSOTHAMNUS BUSH, CA. 4 MILES S.W. OF MOSCA, SAN LUIS VALLEY. RAMALEY (1942: 342). 10 plots, each 3200 sq. ft. (40 × 80 ft.). 7 spp. in all: *S. vermiculatus* (greasewood), *Chrysothamnus* (2 spp.), *Atriplex canescens, Sporobolus cryptandrus, Distichlis stricta, Lepidium alyssoides.* Only 4 species are bushes. Density is low, > 80% of the surface being bare. This community was studied by random spotting of plants in a hypothetical area of the extent given (assuming plots to be contiguous). For each species, individuals in the correct number were located in the manner earlier described. By subdividing plots and finding average species-number for each of 9 sizes of plot, figures for a species-area curve were obtained. They ran, in part, .908 spp. per 50-sq.-ft. plot, 2.15 spp. in 200 sq. ft., 3.15 in 800, 3.8 in 3200, 4 spp. in 6400 sq. ft., and no more than 4 in each larger size up to the total of 32,000 sq. ft. It may be possible that a very much larger area than Ramaley recorded would have the same 4 bush species and no others. This result might be expected if the site excludes most bush species of the district. A more extreme condition may be present in the fine-textured, saline, at times flooded or waterlogged soils of many playas of the Great Basin. Some of these may be habitable only to greasewood. A truly pure stand of one species exhibits the minimum in floristic richness. In the San Luis Valley, some greasewood areas have less extreme environments than the one with 4 species, as Ramaley's second greasewood example shows.

SARCOBATUS–CHRYSOTHAMNUS, 20 LOCATIONS. RAMALEY (1942: 244, TABLE 2). In each of 20 places in the San Luis Valley, Ramaley listed species in 50 0.1-sq.-m. plots. *Sarcobatus* occurs in 440 plots, *Chrysothamnus* in 360, *Atriplex canescens* in 11, *Franseria acanthocarpa* 9, *Gutierrezia* 9, *Senecio spartioides* 7. Ramaley did not separate the different species of rabbitbrush, but mentions that there are more than 6 of them. For species-area treatment, the

360 plots with some species of *Chrysothamnus* are arbitrarily divided among 5 species thus: 234, 86, 21, 13, 6. Excluding herb species in his table, bush species occur in 836 of the 1000 plots, making the number of bush species per plot 0.836. Assuming a total of 900 bushes, with 1 bush covering 5.8 sq. ft. and with bushes occupying 30% of the surface, then 900 bushes occur in 400 mlc., an acre contains 2252 bushes, and 100 bushes occupy 44.4 mlc., with 3.77 spp. (this species-number from a trial section of a species-area graph). By C-conversion from 100 bushes with 3.77 spp., 20 bushes on 8.88 mlc. include 2.57 spp.; 5 bushes on 2.22 mlc. include 1.67 spp. — Unlike the preceding example, this one shows very slow but continuous increase of species with area, with a presumed 6.5 species at 10 acres, 8.2 at 1000 acres (as read from the extended species-area curve). Ramaley's 1000 plots in 20 places with 10 bush species thus sample a very large area, perhaps equivalent to a uniform stand of 5 to 15 square miles.

GRASSLANDS

TABLE 12. Tall-Grass Prairies, and Sand Prairie.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Mesophytic prairie, n.e. Ill.	17.0	68.8	24.7	35.5	3
Af—As facies, Nebraska City, Neb.	6.33	25.6	47.7	68.6	3
As—Af facies, Nebraska City	8.64	35.0	42.5	61.3	2
High prairie near Lincoln, Neb.	6.89	27.9	28.2	42.0	1
Low prairie near Lincoln	7.90	32.0	35.2	53.2	1
Sporobolus—Andropogon, N. D.	14.3	57.9	62.0	89.3	3
A. scoparius type, N. D.	12.0	48.6	36.0	52.2	3
Eragrostis, etc., Havana, Ill.	18.5	74.7	12.7	18.1	1
Pastured bunch grass, Havana	44.3	179.4	17.5	25.9	1
Leptoloma variant, Oquawka	15.0	60.7	17.1	25.3	2
Interdunal flat, Hanover	24.0	97.1	23.9	34.8	3
Lower slope, Hanover	27.6	116.9	22.1	32.9	2
Upper slope, Hanover	18.4	74.6	22.3	32.4	2
Plateau-top, Hanover	70.0	283.1	22.9	33.2	2
Sparse vegetation, blowsand	75.0	303.3	5.59	8.34	3
Calamovilfa type, N. D.	13.0	52.4	30.0	43.0	3

MESOPHYTIC PRAIRIE NEAR ELMHURST, N.E. ILLINOIS. VESTAL (1913: 357). A small relict area of good prairie, including large bunches of *Sporobolus heterolepis,* was preserved in an acute angle between two intersecting railroads, not far west of Chicago. Prairie of this district is characteristic of the fertile dark soils of late Wisconsin glaciation. This area had 35 spp. in 20.66 mlc. A larger area estimated at 70.66 acres, had 80 spp. It includes some variations of site, chiefly dependent on small differences of level and drainage, but species found only in lower spots were excluded from the list. As seen in Table 12, reference areas are larger and species-numbers are smaller than for prairies farther west. One should not infer from this single example that eastern prairies show more severe competition than those in the middle of the prairie region, nor that the eastern prairie flora is more limited.

ANDROPOGON FURCATUS–A. SCOPARIUS FACIES, NEAR NEBRASKA CITY, NEB.
J. J. THORNBER (1901). This early statistical study is still of highest value.
The map permits estimates of the larger areas; numerous detailed enumerations
for 1-sq.-m. quadrats are given. Only 4 plots are reported for this less xeric type,
with the taller bluestem the leading dominant. Plot no. 6, east slope, and nos.
4 and 7, north slope, have the 2 *Andropogons* as dominants. No. 5, west slope,
also has *Panicum virgatum*. In general, little correlation is evident between
exposure and type, or between exposure and no. of spp. For these 4 plots, there
are 29 to 38 spp. (38 in the Af–As–Pv plot, no. 5). Mean species-number
is 32.75. The trend of the curve for this facies was judged from that for the
As–Af type, next mentioned.

A. SCOPARIUS–A. FURCATUS FACIES. THORNBER (1901). This facies has 2
dominants, little bluestem in the lead. There are 8 quadrats, with 25 to 32 spp.;
mean is 27.5. The plots are in various exposures and levels. Lower part of curve
was based on species-numbers for smaller areas than 1 sq. m., found by means
of no. of individuals in Quadrat 1, using C-conversion. Upper part was based
on total of 141 spp. in 155.4 acres of typical prairie (est. from Thornber's map).

A group of types, in some respects intermediate between the drier As–Af and
the less extensive Af–As facies, has the same 2 dominants plus one other. Of
10 such quadrats 3 are As–Af–Bc (*Bouteloua curtipendula*), 1 is Bc–As–
Af, 2 have *Panicum Scribnerianum* as the third dominant, 2 have *Koeleria cristata,* 2 have *Carex pennsylvanica*. Species-numbers, 27 to 35; mean is 29.5. If
these 10 quadrats were considered as representing one type, reference areas and
species-numbers on a curve would surely fall between those for the two types
just given.

HIGH PRAIRIE NEAR LINCOLN, NEBRASKA. T. L. STEIGER (1930). This comprehensive presentation of plot data for two types of prairie is an outstanding
example of the great usefulness of field data when published in detail. It has
already been the subject of statistical treatments by several investigators. In 40
1-sq.-m. quadrats in high prairie, Steiger recorded 43 + 2 species (17 grasses,
28 other herbs). Spp. per plot, ca. 17.4. In a total of several hundred acres.
Steiger listed 81 species (excluding the introduced ruderals); 70 of the 81 species
are characteristic of high prairie. By different combinations of the 40 plots, mean
species-numbers were obtained for 3 other plot sizes: 32.4 spp. in 5 sq. m., 38.8
in 10 sq. m., 48.5 in 20 sq. m. Thus a dependable basis for a curve is assured. —
The plot data include counts of individual plants. Thus in 1 sq. m., mean no. of
grass individuals is 218; of other herbs is 32.2. This is 6.2 sq. inches per plant or
40 sq. cm., or 0.0430 sq. ft.

LOW PRAIRIE NEAR LINCOLN. STEIGER (1930). The article gives similar data
for 40 quadrats in low prairie, with 56 species; and with a total of 75 species
in a general area considerably smaller than that for high prairie. These 75

species also do not include ruderals. 45 of the 75 are characteristic of low prairie; 20 do not occur in the high-prairie area. Mean no. of spp. is 18 in 1 sq. m., 32.4 in 5 sq. m., 38.8 in 10, 48.5 in 20. — Individuals are smaller and herbage is denser in low prairie. Per sq. m., mean no. of grasses is 270.55; of other herbs is 53.3. Ground-space per plant is 4.8 sq. inches, or 31 sq. cm., or 0.0333 sq. ft.

The one Illinois and two Nebraska localities show conclusively one important feature of at least these species-area curves, since each affords a species-number for a large area, 70 to several hundred acres, or *4000* to *58,000* times the minimum area. A curve for any of these localities, if extended to so large an area, convincingly demonstrates that the upper section of a species-area curve cannot have so steep a slope as the middle section. If, for example, the curve for Steiger's high prairie continued at the slope of its steeper middle section as far as 300 acres, the indicated number of species would be 137. Steiger's tally for the whole high-prairie area studied (estimated as 400 acres, possibly no more than 300) is 81. It is inescapable, therefore, that the large-area section of such a curve is convex, with progressive decline in slope at all points beyond the point of flexure. This has been found true in all cases for which large-area tallies are available.

SPOROBOLUS HETEROLEPIS–ANDROPOGON FURCATUS PRAIRIE, WESTERN NORTH DAKOTA. H. C. HANSON AND W. WHITMAN (1938). For each of ten types of prairie vegetation, the authors selected a number of representative test areas, with homogeneity a chief requirement. There are 36 of these test areas, each of 2 to 20 acres. In each test area Hanson and Whitman established 30 scattered 1-sq.-m. quadrats. The average number of species per plot in the 30 plots or quadrats, and the total number of species in the 30 plots, are given for each of the different test areas as part of their Table 1 on page 61.

One test area in each of six of their types was used in the present species-area study. Of 4 localities for the *Andropogon furcatus* type, test area 30 was selected. The type is richer in species than others, and this *Sporobolus–Andropogon* variant in area 30 is richest within the type. It has 86 spp. in the 30 scattered quadrats, and a mean of 20.3 spp. per quadrat. The area is ca. 16 miles n. of Kildeer, near the edge of the "breaks" of Little Missouri River, on lower part of a gentle north slope. Soil is a dark-colored fine sandy loam. The authors considered it the best-developed prairie they studied. The present writer's experience with eastern prairies led him to regard *Sporobolus heterolepis* as an indicator of least disturbed prairie, usually in favorable sites. The best early description of Illinois prairie, by C. W. Short (1845: 191) includes a mention of *Vilfa heterolepis* conveying a similar impression; it is the species most palatable to grazing animals: first to be "eaten out." In addition to this grass and the big bluestem, one or more small xeric grassland species of *Carex, Stipa comata,* and *Calamovilfa* are dominant. — The curve is based on 3 points, one for species-number at 247 mlc. (20.3 spp.); a second point for a one-piece area equal to the aggregate of 30 plots (30 sq. m. or 7.41 mlc., with an estimated 79 spp.);

the third point is for the one-piece area which will include the number of species (86) given for the 30 scattered plots (this area is est. at 11.76 mlc.). Species-numbers for these same three areas are similarly used for each of the other 5 types borrowed from Hanson and Whitman.

ANDROPOGON SCOPARIUS TYPE, NORTH DAKOTA. HANSON AND WHITMAN (1938). Test areas 25 and 26 are of this type. The former is on the lower part of a 20-to-25-degree slope, with dark-brown, fine sandy loam of high carbonate content, on the Olstad Ranch ca. 16 miles s.e. of Sentinel Butte. Spp. per plot, 12.8. 52 spp. in 30 scattered plots or in a one-piece area of 11.76 mlc.

BUNCH-GRASS OF SAND PRAIRIE: ERAGROSTIS–LEPTOLOMA–PANICUM VARI-ANT, ILLINOIS RIVER DUNES. H. A. GLEASON (1907: 160, TABLE 1). Some of the more extensive eastern sand prairies are in the dunes of widened parts of major river valleys, just below terminal moraines of the Wisconsin ice-sheet. Gravels and sands were deposited by the glacial torrents over what now are extensive terraces. Dunes of the Illinois River were studied by Hart and Gleason (1907). Of Gleason's quadrat studies in sand prairie near Havana, Du Rietz wrote (1924: 430, after a paragraph on "Die rein technische Quadrat methode"): "Zu wirklich statistischen Untersuchungen wurde die Quadrat methode wahrscheinlich zum ersten Mal von Gleason (Hart und Gleason 1907, vergl. Du Rietz 1921 p. 102) verwendet; auch in dieser Hinsicht enthält also die Arbeit RAUNKIAERS von 1909 nichts Neues." — Gleason's earlier quad-rats are of generous size, 100 square feet. Tables give details for each individual quadrat, and include abundance data which permit one to find approximate numbers of individuals per quadrat. Abundance classes (with specified limit-ing numbers) are indicated by symbols for particular species in each plot. — The bunch-grass type in Table 1 is dominated by *Eragrostis trichodes, Leptoloma cog-natum*, and *Panicum* species. The area is a strip 110 × 10 ft., of 11 quadrats, with 20 spp. in all. The area of a compact plot (a square) which includes 20 spp. was estimated to be 1500 sq. ft., or 34.4 mlc. One quadrat has 9 to 14 spp.; mean number is 11.09. For small areas, Plot 2 with 11 spp. was "mapped" by random spotting of the proper number of individuals for each sp., and divided into quarter-plots. Arrangements of adjacent whole plots in groups of 2, 3, and 5 brought the number of plot-sizes to 8. The curve fitted to the 8 points has lowest rate of increase among 8 curves for bunch-grass vegetation in sand.

PASTURED BUNCH-GRASS, HAVANA AREA. GLEASON (1907: 161, TABLE 2). No cattle had been on the area during two years preceding Gleason's field study. Dominant grasses were *Bouteloua hirsuta, Paspalum setaceum*, and *Panicum* sp. In a 10-plot strip (100 by 10 ft.), 24 spp. were recorded. Equivalent com-pact area is 31 mlc. Spp. per plot, 12.2. Curve is based on 5 plot-sizes.

LEPTOLOMA VARIANT, OQUAWKA AREA, MISSISSIPPI RIVER DUNES. GLEASON (1910: 62, TABLE 1). For his second article on the vegetation of sand areas in

Illinois, two tracts of dunes along the Mississippi were among those studied. The Hanover area is not far from the northwest corner of the state. The Oquawka area is perhaps 100 miles farther down-stream. — The *Leptoloma* variant is dominated by an eastern bunch-grass allied to *Panicum, L. cognatum*. It is green and leafy, low, and in places almost turf-forming. It has bright-red fine-branched panicles which break off and roll with the wind as tumble-weeds do. It has in many places become dominant along roadsides in sand, and tolerates disturbance of several kinds. In a stand of this grass Gleason listed species in a strip of 10 quadrats, each 2 m. square. 25 spp. in all; 10.6 spp. per plot; 5 sizes of plots or aggregates. *Paspalum* and *Bouteloua, Ruellia ciliosa, Baptisia bracteata, Ambrosia psilostachya,* and *Monarda punctata* are notable in the list. This and most of Gleason's later enumerations were frequency data: for each column representing a quadrat, occurrence was noted for each species present by a symbol.

MIXED BUNCH-GRASS, INTERDUNAL FLAT, HANOVER AREA. GLEASON (1910: 66-67). In a series of sites beginning southwest of the Hanover railroad station, Gleason studied variations of mixed bunch-grass in different slopes and levels. The densest vegetation was in a flat area between dunes. Since in this area as well as the others, more than 2 or 3 bunch-grass species were important, Gleason named this type the mixed consocies.* The 8 bunch-grasses and 1 sedge of the flat include two dominants, *Leptoloma* and *Koeleria,* which occupy more space than all the others (*Stipa spartea, Sorghastrum,* 3 species of *Panicum, Carex Muhlenbergii,* and *B. hirsuta.* Other notable plants are *Selaginella rupestris, Callirrhoe triangulata,* and *Tephrosia virginiana.* A census of 10 plots, each 2 m. square, was made. Gleason recorded 29 species in the plots, 11 others outside. — Compact area to yield 40 spp. is est. at 58 mlc. Mean species-number per plot of .988 mlc. is 12.1. The curve for this interdunal flat shows fewer species at small areas than does the upper part of the slope beyond the flat, but probably more species at sizable areas.

MIXED BUNCH-GRASS, LOWER SLOPE, HANOVER. GLEASON (1910: 69, TABLE 2A). Through the slope beyond the flat, Gleason surveyed a line of 20 plots in the lower part and 20 plots in the upper part. Each plot is 0.5 meter square. In the lower part, bare-sand spaces between grass bunches were small. *Leptoloma, Panicum pseudopubescens, P. perlongum,* and *Koeleria* are the dominants. *Andropogon scoparius, Sorghastrum,* and *Callirrhoe* are among the other plants. Species per ¼ sq.-m. plot, 2.5. In all 20 plots, 14 spp. 3 intermediate plot-sizes.

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* In both 1907 and 1910 articles, a variant or facies of some plant association, characterized by some one or a few dominants, was designated a *consocies.* This was in the period before Clements had narrowed the meaning of this term by associating the ending -ies with temporary status in a succession, and before the erroneous idea had become wide-spread that a consocies in the original sense or its later equivalent *consociation* could have only one dominant. Ecologists should take note of the original signification of consocies, which was the generally understood meaning before about 1920.

MIXED BUNCH-GRASS, UPPER SLOPE, HANOVER. GLEASON (1910: 69, TABLE 2B). Here the vegetation is more open, interspaces are larger, leaving more room for interstitial annuals and other plants which do not compete well with the bunch-grasses. The effect is to increase no. of spp.: av. per plot, 4.3 spp.; in all 20 small plots, 16; frequencies of occurrence-in-plots of all species except *Leptoloma* are higher. Dominants are *Leptoloma, B. hirsuta, A. scoparius, Koeleria, P. pseudopubescens. Aster linariifolius* is frequent. *Talinum rugospermum* is in 1 plot. 6 plot-sizes.

MIXED BUNCH-GRASS, PLATEAU-TOP, HANOVER. GLEASON (1910: 70). On the elevated surface beyond the slope, 10 plots, each of 4? sq. m. Spp. per plot, 9.4. 22 spp. in the plots; 14 other spp. outside the plots. Estimate of area examined (with 36 species), is 110 milacres. Species-numbers at a given area on this upland are smaller, and reference areas are larger, than for other sites in the mixed consocies. The reference areas are smallest in the upper-slope site, perhaps because there is less competition there than there is in other locations.

SPARSE VEGETATION OF BLOW-SAND, HAVANA AREA. GLEASON (1907: 166-167, TABLES 5-7). These tables give the plant census for three typical areas of blow-sand, which is nearly bare, with surface drift of wind-blown particles and usually very sparse cover of annuals, as *Cassia chamaecrista, Cenchrus, Commelina,* the rare viscid herb *Cristatella Jamesii,* and of scattered or locally abundant shoots of *Ambrosia psilostachya,* from its rhizomes an inch or two below the surface. In each area 5 quadrats, each 10 ft. square, were recorded. The composite data served as basis for species-numbers for 6 plot-sizes. Numbers of spp. in the 3 groups of plots: 5, 7, 4; in all 3 groups, 8. Spp. per 100 sq. ft, 2.93. Estimated compact area to include 8 spp., 52 milacres.

CALAMOVILFA TYPE, NORTH DAKOTA. HANSON AND WHITMAN (1938: 78-80, 94). *C. longifolia* is a tall coarse-textured bunch-grass distinctive of sand (either loose, or stabilized somewhat loamy sand). It is chiefly found in sand prairie, as in sandy plains east of Denver. In North Dakota it "occurs widely on sandy ridges and hills"; it is frequent in the river dunes of Illinois. It is also widely distributed along sandy upper beaches of Lake Michigan and Lake Huron. Hanson and Whitman record it as a distinctive prairie type, giving records from Test Areas 21 to 24: 35 to 42 spp. in 30 1-sq.-m. quadrats, with 9.9 to 12.6 spp. per quadrat. A curve was drawn for Area 21, richest in species of the four. It is on a sandy upland ridge on Olstad Ranch, ca. 16 miles southeast of Sentinel Butte. Soil is fine sand to sandy loam. Other plants are *Andropogon Hallii,* a bunch-grass also characteristic of sand, *Meriolix, Yucca glauca.* One-piece area equiv. to 30 scattered quadrats (as in other cases) is est. at 11.75 mlc.

TABLE 13. Grasslands of Great Plains and Mountain Border

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Bouteloua—Stipa—Carex type, N. D.	16.2	65.6	32.5	46.8	3
Agropyron—Bouteloua—Carex type, N. D.	1.10	4.45	9.95	14.3	3
Plains near Browning, Montana	2.26	9.15	14.2	20.5	3
Grassland at Glacier Park, Montana	5.03	20.4	14.1	20.4	3
Meadow near Palmer Lake, Colorado	10.5	42.5	22.2	32.1	3
Mesophytic prairie, Palmer Lake	4.71	19.1	22.4	32.2	3
Short-grass with bushes, near Boulder	7.14	28.9	22.7	34.0	2

BOUTELOUA–STIPA–CAREX TYPE, NORTH DAKOTA. HANSON & WHITMAN (1938: 61, 63-68). This extensive type, No. 1, occupies level or moderately sloping areas, mostly of sandy loams developed from sandstones or from materials eroded from former buttes or hills. *Bouteloua gracilis, Stipa comata,* and a grassland species of *Carex* are the usual dominants. The authors give data for Test Areas 1-3, 4, 6, and 7, with 10.9 to 19.2 spp. per 1-sq.-m. quadrat, and with 33 to 53 spp. in 30 scattered quadrats. Data for Area 6 were used for a curve. No. 6 has 11.5 spp. per plot; 44 spp. in 30 plots. It is on a gentle north slope, 26 miles southwest of Belfield on road to Ranger.

AGROPYRON–BOUTELOUA–CAREX TYPE, NORTH DAKOTA. HANSON & WHITMAN (1938: 69-71). Type 2 is in fine soils, clay loam to clay, on long, gradual slopes. Carbonate accumulations are not far below the surface. Test Areas 10-13 have 3.7 to 11.0 spp. per quadrat, 12 to 29 spp. in 30 plots. Area 10, used for an S-curve, has good representation of all 3 dominants, *A. Smithii, Bouteloua,* and *C. filifolia.* Absence of *Stipa,* which is characteristic of coarse soils, is apparently an indication of this type. Area 10 is 11 miles northeast of Sentinel Butte. It has 10.3 spp. per plot, and 20 spp. in 30 plots.

PLAINS NEAR BROWNING, NORTHWEST MONTANA. VESTAL, JULY, 1914. The reservation of the Blackfeet Indians lies east of the front of the Rocky Mountains and just south of the international boundary. The principal village, Browning, is about 14 miles from the mountains. A few miles north of Browning, plains vegetation at about 3000 feet elevation comprises at least four types: a xeric extreme, moist meadows of low ground, and intermediate grassland (the extensive type), and a hill prairie on south slopes of sizable hills. Presumably this last site has a longer growing season, permitting the presence of Columbia Basin species. In the extensive type the chief grasses are *Agropyron* species, *Koeleria,* and *Stipa comata,* all of reduced stature. *Selaginella densa* and *Artemisia frigida* are in spots abundant, almost dominant. *Carex stenophylla* and a *Sporobolus* occur locally. Other *Artemisias, Astragalus* species, a *Rosa, Penstemon, Gaillardia, Chrysopsis, Lithospermum, Liatris, Sphaeralcea coccinea,* a *Gaura,* and species of *Eriogonum, Solidago,* and *Aster* are notable. — In a plot of 144 square ft., 22 spp. In one acre, an est. 36 spp.

Grassland at Glacier Park, Montana. Vestal. July, 1914. This is practically closed prairie-like grassland, few plants exceeding 12 inches height in the drier, more extensive sites, to 18 inches in less-dry places. The prairie occupies terraces and low rolling hills of the mountain-border. The area most studied was southeast of the railroad station, on the west side of Two Medicine Creek. Grassland alternates with groups of aspen and of lodgepole pine. Los spots and aspen borders include tall-herb species. South slopes show a temperature-variant with more of the Columbia Basin species such as *Balsamorhiza sagittata*. One of these, the bunch-grass *Agropyron spicatum*, is the chief dominant over the general area. Other grasses are *A. violaceum, Koeleria*, and species of *Danthonia, Poa, Bromus*, and *Phleum*. Herbs include species of *Potentilla, Aragallus, Lupinus, Peucedanum, Penstemon, Campanula, Achillea, Erigeron, Eriogonum, Heuchera, Lathyrus, Phlox, Artemisia, Chrysopsis, Agoseris. Selaginella densa* is local.—In 120 sq. ft., 18 spp.; in 1 acre, 35 spp.

Meadow near Palmer Lake, Colorado. Vestal, July, 1913. The divides between major streams running out from the mountains are much higher and receive more rainfall than other parts of the eastern border of the Southern Rocky Mountains. One such high divide is near the Wyoming-Colorado boundary. The next is the Platte-Arkansas divide some 60 miles south of Denver, with Palmer Lake, the station, at its summit. The lava-capped mesas at the New Mexico boundary form the third high divide. Mountain plants, including the conifers, extend far east of the mountains on these divides. At Palmer Lake, (elev. 7237 ft.) the grasslands show several types, including meadow in low ground, a mesophytic mixed prairie in well-drained sites, and patches of mountain bunch-grass in some rocky or gravelly spots on cliffs or tops of buttes. The meadow studied was near the railroad, north of the station. *Phleum pratense* was the abundant grass, with *Poa, Agropyron*, and *Muhlenbergia*. There were also a *Juncus, Sisyrinchium angustifolium*, and *Allium recurvatum;* and numerous dicot herbs, including *Potentilla, Thermopsis, Lathyrus, Rudbeckia, Aster*, and *Achillea.* — A small area of 36 sq. ft. had 17 spp.; a larger area estimated at 324 sq. ft. had 30 spp.

Mesophytic prairie, Palmer Lake, Colorado. Vestal, July, 1913. (For a description of local mountain-border prairies, see Vestal, 1914: 390.) This rather dense grassland was just above the meadow of the preceding paragraph. The dominant grass was *Stipa viridula*, with *Agropyron Smithii, Koeleria*, and a *Bromus. Calochortus gunnisonii, Geranium Parryi, Galium boreale, Lupinus argenteus, Erigeron macranthus*, and species of *Artemisia, Aster, Cirsium, Monarda*, and *Rosa* were conspicuous. — In 60 sq. ft. there were 25 spp., and in 484 sq. ft., 38 spp.

Short-grass with bushes, east of Boulder, Colorado. Vestal, September, 1912. The "bushes" are barely more than suffrutescent herbs. See description in later section on mixed vegetation.

TABLE 14. Mountain and Intermont Grasslands, Colorado.

Stand or type		Am, *mlc.*	Am, *sq. m*	Sr	Sm	D
Foothills n.w. of Boulder, 7000 ft.		16.5	56.8	30.3	43.7	3
Upper Arkansas valley, Buena Vista		10.7	43.3	14.8	21.9	3
Mountain park grasslands, Tolland, 8800 ft.						
Erigeron multifidus	ridge	6.31	25.5	22.7	32.9	3
Muhlenbergia—Comandra	slope	10.0	40.5	32.3	46.2	3
Muhlenbergia—Antennaria	slope	6.78	27.4	35.9	51.9	3
Muhlenbergia—Aragallus	slope	6.81	27.6	30.9	44.8	3
Muhlenbergia—Danthonia	less xeric slopes	8.25	33.4	32.2	46.7	3
Grassland of glacial sink		6.08	24.3	35.3	52.0	3

FOOTHILL MIXED GRASSLAND, N.W. OF BOULDER. 7000 FT. ELEV. VESTAL (1917: 373-375). The station is on an east slope below the top of a round-topped granite hill 2 miles west of the mountain front. Abundant species are *Bouteloua gracilis, Phacelia heterophylla, Chrysopsis, Senecio oblanceolatus, Geranium Parryi, Artemisia frigida, Aragallus Lambertii.* Also notable are *Koeleria, Mertensia lanceolata, Carex pennsylvanica,* and species of *Lesquerella, Linum, Gilia, Helianthus, Eriogonum, Gaillardia,* and *Townsendia.* — 24 spp. in plot 8 × 8 ft. (1.47 mlc.). Est. no. of spp. in one acre, 72.

SUBMONTANE DRY GRASSLAND, INTERMONT PLAIN OF UPPER ARKANSAS VALLEY, AT BUENA VISTA. 7950 FT. ELEV. VESTAL, JUNE, 1914. The area studied is close to the town, west of the river. It is flat, with coarse soil and a few surface rocks. The dominant grass was *Bouteloua gracilis. Artemisia frigida* was abundant, locally dominant. Frequent plants were *Sitanion brevifolium, Hymenoxys floribunda* (Colorado rubber plant), an *Erigeron,* a *Sideranthus,* and small bushes of *Eriogonum effusum.* Numerous less frequent species included *Opuntia polyacantha, Echinocereus viridiflorus, Selaginella densa, Erysimum, Hymenopappus.* — 12 spp. at 48 sq. ft. (1.10 mlc.) ; 27 spp. at ca. 2000 sq. ft. (45.9 mlc.)

This grassland has been modified by grazing, and bears considerable similarity to the grassland with bushes on a rocky mesa-top east of Boulder, described in a later section on mixed vegetation.

MONTANE PARK GRASSLANDS, MIDDLE BOULDER PARK, NEAR TOLLAND. 8800 FT. ELEV. F. RAMALEY (1914, 1915, 1916). Ramaley had in earlier papers briefly described the dry grasslands of the stony floor of this small glaciated plain surrounded by mountains. Meadows in the flood-plain, sedge moors and willow thickets bordering the stream (Middle Boulder Creek), and occasional single trees or conifer groups, are the other kinds of vegetation in the park. In the 1915 article, Ramaley gave details for 16 grassland quadrats, each 1 sq. m., as percentages of cover for single species (or in some cases for 2 or 3 species of one genus). The high variability of composition shows in number of species per

plot: the range is from 9 to 23. It can hardly be said that there is any modal number of species. These species-numbers were used in estimating likely numbers of species per plot for the sections of strips of plots in Ramaley's 1916 paper. In this he described an east-west line of 138 quadrats, with an additional row of 20 plots starting from plot 45 in the main strip. There are six variants, depending on topography and exposure. Data for the six variants do not include details for individual plots. Cover percentage is given for different species, in each variant and in the 158-plot aggregate.

ERIGERON MULTIFIDUS SOCIETY. ON XERIC RIDGE, PLOTS 1-16. Dominants are *Koeleria, Carex stenophylla,* and *Aragallus Lambertii.* Est. mean no. of spp. per plot, 12. 32 spp. in 16 plots. Est. equiv. compact area, 22 sq. m. or 5.44 mlc.

MUHLENBERGIA–COMANDRA SOCIETY. XERIC SLOPE, PLOTS 37-76, 139-158. The most extensive variant. *M. gracilis* and *Comandra pallida; Artemisia frigida,* and *Chrysopsis villosa* are the important species. Spp. per plot, ca. 13. 54 spp. in 60 plots. Est. equiv. compact area, 108 sq. m. or 26.7 mlc.

MUHLENBERGIA–ANTENNARIA ANAPHALOIDES SOCIETY. XERIC SLOPE, PLOTS 17-31. *Festuca saximontana, Chrysopsis,* and *Cerastium occidentale* are important. Spp. per plot, ca. 19. 49 spp. in 15 plots. Est. equiv. compact area, 20.3 sq. m. or 5.02 mlc.

MUHLENBERGIA–ARAGALLUS SOCIETY. XERIC SLOPE, PLOTS 92-110. *M. gracilis* covers 14.8% of area, *Koeleria* 6.7%, *A. Lambertii* 5.4%. *Danthonia Parryi* and *Artemisia* are also important. Spp. per plot, ca. 16. 45 spp. in 19 plots. Est. equiv. compact area, 28 sq. m. or 6.92 mlc.

MUHLENBERGIA–DANTHONIA SOCIETY. ON 3 HYPOXERIC SLOPES, PLOTS 32-36, 77-91, 127-138. *Festuca saximontana* with 11.9% cover, *D. Parryi* with 6.4%, and *Cerastium* with 3%, are important. Spp. per plot, ca. 15, 57 spp. in 60 plots. Est. equiv. one-piece area, 120 sq. m. or 29.7 mlc.

DANTHONIA INTERMEDIA VARIANT, OCCUPYING GLACIAL SINK. PLOTS 111-126. *D. intermedia* has 9.2% cover; *Muhlenbergia gracilis* has 11.8%. Spp. per plot, ca. 18. 50 spp. in 16 plots. Est. equiv. compact area, 22 sq. m. or 5.44 mlc.

COLUMBIA BASIN GRASSLANDS

A distinctive prairie-like formation occupies parts of the northern Great Basin, and of lower to middle elevations of included and bordering mountain ranges, as well as numerous intermont plains of those mountain districts. Infusions of its flora are found in the plains of British Columbia; east through the Rocky Mountains in Montana, Wyoming, and northern Colorado; west of the Cascades as far south as Shasta Valley, and southwest as far as the east slopes of the southern Sierra Nevada. This grassland has less severe winters and drier

summers than Great Plains and prairie grasslands east of the mountains. Absence of species of *Andropogon* and *Bouteloua;* dominance or abundance of *Agropyron spicatum, Festuca* species, *Balsamorhiza, Wyethia,* etc., are characteristic.

TABLE 15. Columbia Basin Grasslands.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Dry prairie, Wild Horse Island, Montana	12.55	50.4	17.5	26.2	3
Openings, Osprey Island, Montana	5.37	21.7	14.2	21.3	3
Agropyron—Poa, Garfield Co., Wash.	0.799	3.15	12.08	17.7	3
Agropyron—Poa, Franklin Co., Wash.	1.255	5.08	11.61	17.1	3
Festuca—Agropyron, Whitman Co., "B."	2.39	9.68	23.7	34.6	2
Festuca—Agropyron, Whitman Co., "A"	4.60	18.6	22.5	32.7	2

DRY PRAIRIE, WILD HORSE ISLAND, FLATHEAD LAKE, N.W. MONTANA. VESTAL, JULY 2, 1914. Grasslands of the northern-Great-Basin type occur on adjacent lands south and west of this large lake, and scatteringly in a narrow thermal belt on the west flank of the Mission Range (east of the lake). Wild Horse Island is several miles long, and is in the large bay on the west side. Dry grass-covered low hills occupy much of its area. Relatively few species occupy the driest high and more exposed sites. Draws and depressions are wet in spring, but are mostly dry by midsummer. In the intermediate sites, to which this description applies, almost all species of the grassland list are found. *Agropyron spicatum* is the chief dominant. *Koeleria,* other *Agropyrons,* and species of *Elymus, Poa, Festuca,* and *Aristida* are relatively infrequent. *Balsamorhiza sagittata* (balsam-root), a *Helianthella,* species of *Lupinus* and of several umbelliferous genera; *Chrysopsis, Artemisia, Erigeron, Achillea, Agoseris, Castilleja, Allium, Zygadenus, Calochortus,* are conspicuous. *Lewisia rediviva* (bitter-root) and *Clarkia pulchella* (appropriately named for the explorers of the northwest) are characteristic. Moderately or less frequent are species of *Eriogonum, Sieversia, Potentilla, Phacelia, Campanula, Antennaria.*—14 spp. in 64 sq. ft. or 1.47 mlc.; 31 spp. in a larger area est. at 1800 sq. ft. or 41.3 mlc.

OPENINGS, OSPREY ISLAND, FLATHEAD LAKE. VESTAL, JUNE 27, 1914. This small island in the south part of the lake was largely forested. There and in forests east of the lake are many openings with mixed herbaceous cover of plants from open forest, meadow, and dry grassland. (Many mesophytic herb species occur equally in meadows and in openings.) Surrounding woody plants are *Pinus ponderosa, Pseudotsuga, Ceanothus, Physocarpus, Symphoricarpos, Ribes.* In two similar and nearby openings: *A. spicatum* dominant, *Balsamorhiza, Koeleria,* a tall *Poa, Peucedanum* or *Cogswellia, Allium, Erysimum, Penstemon, Berberis aquifolia* (woody at base), *Fragaria,* etc. (In other clearings: *Pteridium, Carex* spp., *Collomia, Clarkia pulchella, Heuchera, Chamaenerion, Antennaria, Vicia, Collinsia, Galium, Hieracium, Castilleja,* etc.)—13 spp. in 36 sq. ft., or .826 mlc.; 24 spp. in ca. 500 sq. ft. or 11.48 mlc.

AGROPYRON SPICATUM–POA SECUNDA ASSOCIATION, S.E. WASHINGTON. R. F. DAUBENMIRE (1942: 64-68). *Agropyron* forms large bunches, 37 to 40 per milacre. There are also occasional large herbs, the small bunchgrass *Poa secunda,* and large numbers of small annuals covering much of the ground between larger plants. This association is developed in a wide belt between the *Artemisia–Agropyron* association of drier plains to the northwest and west and the *Festuca–Agropyron* association of less xeric country closer to the Bitterroot and Blue Mountains. Daubenmire gives descriptions of two undisturbed stands, one near the less xeric eastern edge of the *Agropyron* belt in n. Garfield Co., the other near the xeric western edge in e. Franklin Co. His Table 3 gives frequencies in 100 small plots for each stand. Plots are 2 $\times$ 5 dm., arranged in rows with plots separated by 1 meter. From total of occurrences in plots, the mean no. of spp. per plot is 8.57 for Garfield Co. (G), 7.00 for Franklin Co. (F). No. of spp. in 100 plots is 24 in G, 22 in F. The one-piece area equivalent to the plot-aggregate was estimated on the assumption that plot-rows were well separated: the value computed is 296 plot-units or 7.32 mlc. Only 6 other stands or types among 55 grasslands studied have with these two an Am value smaller than 2 mlc. The much smaller Am of G (.779 mlc.) than of F seems to be partly the result of a richer complement of species among the small annuals (16 in G, 12 in F, Daubenmire states). Higher density of individual plants may also contribute.

FESTUCA IDAHOENSIS–AGROPYRON SPICATUM ASSOCIATION, S.E. WASHINGTON. DAUBENMIRE (1942: 70-74). This more nearly mesophytic grassland has the spaces between dominant grasses occupied by large dicot herbs. Conspicuous among these are *Balsamorhiza sagittata, Lupinus, Potentilla, Sieversia, Geranium, Hieracium.* Species of high constancy include *Calochortus elegans, Clematis hirsutissima, Frasera albicaulis, Orthocarpus tenuifolius,* and *Zygadenus gramineus.* As in the preceding community, Daubenmire established 100 small plots in each of two undisturbed stands. These are in Whitman County, about 8 km. apart One is just east of Pullman, and is shown in his Fig. 13. In each stand the frequency plots (Table 8) are 2 $\times$ 5 dm., arranged in 2 rows 1 meter apart, with 1 meter intervals between plots in a row. For this arrangement the estimated one-piece equivalent area is 5.93 mlc. (240 plot-units). Av. no. of spp. per small plot is 9.12 in stand A, 13.77 in B. Species in the 100-plot aggregate number 37 in stand A, 42 in B. Daubenmire gives additional data in each stand for areas of 1 to 10 sq. m. in a strip 1 meter wide, 10 meters long. His Table 7 shows for A, 22 spp. in the first 1-sq.-m. plot of the strip, 24 spp. in plots 1 and 2, 25 spp. in plots 1 to 6, etc. For the whole strip there are 29 spp. — The strip for stand B shows 24 in the first plot, 26 in 1 and 2, . . . to 31 spp. in the 10 plots. The compact area (no longer than wide) estimated to be equivalent to a 1 $\times$ 10 strip is 11.5 plot-units, with area in this case 2.84 mlc. For each stand two sets of points were thus available for plotting curves: 2

points from the group of 100 0.1-sq.-m. plots, 10 from the strip of 10 1-sq.-m. plots. Since the second set is not an average of replicated data, agreement is not very close. Daubenmire concluded that "the great bulk of the species in the stand is encountered in a single, random, meter-square plot. . . ." The species-area curves suggest that the number of species found in his first square meter ordinarily requires 2 sq. m. in Stand B, 8.5 sq. m. in A. The *average* square meter (as shown on the curve) has 20 spp. in B, 15.2 in A. An increase of area to 10 sq. m. brings no. of spp. to 34.8 in B, to 28.9 in A. It is interesting that the number of species Daubenmire observed in the first square meter is close to the Sr value determined by the curve (24 observed and 23.7 on the curve for B; 22 and 22.5 for A). The first 20 to 24 species encountered are sure to include many of the most important species of the community, so that Ar, the smallest representative area, is likely to satisfy some or most of the criteria which some students of vegetation might deem to be requirements for a minimal area. The area 5 Ar, or Am, thus seems to be a fairly conservative standard for minimum area.— Daubenmire noted (p. 72) that minimal area should be smaller in the *Agropyron–Poa* association than in the one dominated by *Festuca*.

DESERT GRASSLAND, SOUTHEASTERN ARIZONA

	Am, *mlc.*	Am, *sq. m*	Sr	Sm	D
Grassland composite, Santa Rita Reserve	29.3	118.7	26.8	40.1	3

DESERT GRASSLAND, SOUTH OF TUCSON, ARIZONA. D. GRIFFITHS (1904). The map on p. 17 of this early study of sparse herbage in overgrazed range shows location of plots in a 49-square-mile tract within what was then the Santa Rita Forest Reserve. It is on the northwest foot-slopes of the Santa Rita Mountains. The present Range Reserve is larger than the early tract. The range was then overgrazed; after it was fenced, and cattle for a time excluded, the perennial grasses recovered rapidly. — As described in the bulletin, surface conditions and plant cover were extremely varied over the tract. Few perennials were encountered in the plots studied. The most frequent species listed, in descending order, are: *Lotus humistratus, Gilia floccosa, Plantago ignota, Eremocarya micrantha, Eriocarpum gracilis, Bouteloua bromoides, B. Havardii, Linanthus aureus, B. aristoides*. Moderately frequent species of *Aristida, Eriogonum, Astragalus, Eriophyllum,* and *Lupinus* are also present. — The plots were 7 × 3 ft. (0.4822 mlc.) 17 plots, A to Q, were recorded in spring, when winter annuals were evident; 11 plots, A' to K', in late summer. Selection of later plots was apparently unrelated to that of spring plots. Details are given on pp. 26-29. A few representative plot descriptions: C (n.w. part), "on a stony ridge in an area cut with steep, shallow ravines," (9 plants in 5 spp., dry weight 19 grains) ; E (w. part), "gently sloping grassy area at upper edge of heavier mesquite brush,"

(423 plants, 8 spp., 1710 grains); G (w. part of s. end), "old grassy area with mesquite" (883, 13, 2128); F' (e. part of s. end), "Sandy alluvial bank about 8 ft. above shifting sands" (1182, 3, 2455). — To simplify the statistical treatment of these plot data, a table was made of occurrences of the 62 species in the 28 plots. Separate frequency percentages for spring and summer were computed. Average no. of spp. per spring plot, 6.88; per summer plot, 3.57. A method of combining spring and summer data indicated that if the same plots had been surveyed at both seasons the combined no. of spp. per plot would average 9.37. — For a species-area curve, aggregates from the 17 spring plots in 2-, 5-, and 12-plot units, as well as the average for 1 plot and the total for 17, were used. When plots are remotely scattered, the one-piece area equivalent to a plot-aggregate can be very large. Thus the one-piece area roughly estimated to include the 46 species recorded for the 17 separated plots is as big as 101 plots (52 mlc.). It is emphasized that the curve, and reference areas from it, apply to a composite of varied grasslands, not to a particular desert-grassland type. The 62 species encountered in Griffiths' 28 plots make a very small sample of the grassland part of the vegetational complex and of the rich grassland flora of the district studied.

Plot data giving actual counts are of value for many purposes; since those are less commonly provided in descriptions of grasslands, the details given by Griffiths will be especially useful. His numbers of individual plants per plot (21 sq. ft.), range from 4 to 8065. Entire count in 28 plots is 24,074. Mean density per plot is 860; per sq. ft., 40.94; per sq. m., 440.8; per milacre, 1783.

For herbaceous cover in creosote-bush desert of another Arizona district and of a California location, see p. 99.

GRASSLANDS IN EUROPE

Grasslands and other herbaceous types have been the earliest and the most frequent materials in plot studies of species and area. These studies were preceded by an interest in the general relation between extent of a natural geographic unit and the richness of its flora. Alphonse De Candolle's two-volume work on plant geography (1855, Chap. 7) expressed this relation clearly, and gave figures to illustrate it. Jaccard's early work (1902) advanced the knowledge of this relation, and Alvar Palmgren illustrated it in detail in his studies of the Åland archipelago (1917, 1922, 1925). Jaccard (1908, 1914) gave the subject a degree of precision by narrowing it to a specific study of measured areas within a stand of a particular, more or less homogeneous, community. It was considered interesting to make species-area curves from Jaccard's original plot data for subalpine grasslands in the Alps.

Du Rietz (1924: 31) states that the first grasp of the Minimiareal problem, i.e., of the fact that an association needs a certain area to give its most important species enough room, is found in Braun (1913) and Palmgren (1917).

Many of the central-European studies from about 1910 and thereafter con-

tain association-tables and other sets of data which should afford much material for species-area curves. Braun-Blanquet and others have studied minimal area from a point of view somewhat different from that of the present essay. Du Rietz and his associates in northern Europe emphasized the constant species (or what might be called first-order constants) in determining *Minimiareal*.

TABLE 16. Grasslands in Switzerland.

Stand or type		Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Subalpine prairies, Ormont:	Area I	4.40	17.8	36.9	55.2	2
	Area III	3.77	15.3	32.1	47.6	2
	Area IV .	3.86	15.6	29.4	42.9	2
	Area VIII	1.74	7.42	22.9	33.7	2
Prairie near Chasseron, Jura Vaudois		9.21	37.3	45.0	66.4	1
Elynetum, central Alps (composite)		3.10	12.5	21.85	31.4	2
Caricetum mucronatae, n. Kalkalpen		0.48	1.94	19.1	27.8	3

SUBALPINE PRAIRIES, UPPER PART OF GRANDE-EAU VALLEY, COMMUNE D'ORMONT-DESSUS, ALPES VAUDOISES, 1050-1200 M. ELEV. PAUL JACCARD (1908). Nine groups of 1-sq.-m. plots, ca. 1 km. distant from one another, were situated "sur un terrain d'alluvion." Five are on slopes, four on level areas. 91 herb spp. were recorded on the 52 plots. The generally distributed species include *Trifolium pratense, Alchemilla pratensis, Chrysanthemum leucanthemum, Festuca pratensis, Dactylis glomerata, Leontodon hispidus, Campanula rhomboidalis, Trisetum flavescens, Anthoxanthum odoratum, Avena pubescens.* The 4 localities here treated, with species distinctive for each, are: I. S. slope at 1190 m.; *Plantago lanceolata, Carex sempervirens, Primula elatior.* III. N. slope at 1050 m.; *Deschampsia caespitosum, Knautia arvensis, Ranunculus montanus.* IV. W. slope at 1160 m.; exuberant prairie, fertilized; *Melandrium silvestre, Bromus erectus.* VIII. Prairie on level area; *Plantago media, Lotus corniculatus, Sanguisorba minor (dictyocarpa).*
A few of the statistics serving as the basis for the species-area curves are:

Locality	Species per plot		No. of Plot-sizes	Largest size, *mlc.*	No. of species
	Range	*Mean*			
I	22-35	28.25	8	1.98	53
III	25-31	27.13	8	1.98	45
IV	23-26	24.67	6	1.48	39
VIII	22-26	23.86	7	1.73	36

SUBALPINE PRAIRIE NEAR CHASSERON, JURA VAUDOIS. 1300-1350 M. ELEV. JACCARD (1914: 12). Jaccard recorded 25 1-sq.-m. plots in 2 up-slope rows on a mountain flank s. of Chasseron. He does not give a list of the species, of which there were 66 on the 25 sq. m. It was estimated that a compact plot of the same

area would have 61 species. Mean no. of spp. per 1-sq.-m. plot is 30. For 2, 3, 5, and 10 sq. m. the numbers are 34.8, 36.4, 39.0, and 45.0. On a later page he states that on 100 sq. m. the species number is 78; on 200 sq. m., 85. — The floristic mixture is richer and reference areas are larger than in any of the Grande-Eau localities.

Jaccard gives in the same article a detailed description of the *Pierrier de Sandalp*, which may perhaps be regarded as an inceptive grassland of stony alluvium. It and the sparse vegetation of his *Arête rocheuse de Sandgrat* were used for curves; the results are in a later group of communities of rocky surfaces.

ELYNETUM, 15 LOCALITIES IN CENTRAL ALPS. 2330-2750 M. ELEV. J. BRAUN-BLANQUET (1932: 70-72). In a comprehensive association-table, details of area and of species number are given for this fine-textured alpine carpet dominated by the sedge *Elyna myosuroides*. Areas of 2 sizes are given for 10 of the locations. 13 locations are in East Grisons, 2 are in South Tirol. 11 species of lichens and mosses are omitted from the treatment, which consisted first in plotting on semi-logarithmic paper all points representing a species-number in a stated area. Points for the same location were joined by fine lines. From this array four points were estimated which represent a median trend through the swarm of given points. These are: 18.0 spp. at 1 sq. m., 24.4 at 4 sq. m., 34.3 at 20, and 38.1 at 40 sq. m. An S-curve through these four points is a composite curve for a generalized Elynetum. The width of the swarm in the first graph is such that reference areas for particular stands could be considerably larger or smaller than those determined for the composite curve. The minimum area from this curve is 3.10 mlc. or 12.5 sq. m. Braun-Blanquet does not mention his own value for minimal area of Elynetum, but indicates on p. 57 that it is larger than 4 sq. m. He states on p. 55 the minimal area for the mountain sedge meadow CURVU-LETUM (10 sq. m.), and for the mountain bunch-grass FESTUCETUM HALLERI (20 to 25 sq. m.). — These minimal areas of Braun-Blanquet are in the same range of magnitudes as the Am-values for mountain grasslands in Table 16.

CARICETUM MUCRONATAE, N. KALKALPEN. H. GILOMEN (1926). In this species-area study, Gilomen used plot-sizes 0.25, 1, 4, 16, and 64 sq. m. Details of species, and of numbers and arrangements of plots, are omitted from the condensed report. Data are included for one of the four communities studied. For this, the *Carex mucronata* association of calcareous sites in high mountains, species-numbers are 16.9, 24.8, 34.8, 36.4, and 37.8. These values were plotted directly. The S-curve of regular form which was tentatively drawn comes far from fitting the plotted points, but seems, until more data are available, as likely as any other. The resulting Am value, 0.48 mlc. or 1.942 sq. m., is the smallest found for any grassland.

TABLE 17. Grasslands: Denmark, Esthonia, Poland, Russia.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Maaløv Krat, Denmark: 1-year Græsmark	1.87	7.55	21.7	31.4	3
8-year Græsmark	1.69	6.82	18.8	27.2	3
Markskellene	3.70	15.0	38.7	56.9	3
Festuca rubra on peat, Esthonia	4.70	19.0	21.4	31.8	2
Festuca rubra on loam, Esthonia	2.36	9.56	28.8	42.0	3
Prairie near Cracow: 1st example	1.63	6.56	21.9	31.8	2
2nd example	3.22	13.0	20.4	29.8	2
Steppe, District and Govt. Voronezh	15.1	61.1	57.8	83.7	3
Avena meadow steppe, Govt. Saratov	13.8	55.6	34.7	51.1	3

GRASSLANDS AT MAALØV KRAT, DENMARK. RAUNKIAER (1910: 45-55, TABLE 10). These grasslands of formerly cultivated fields were sampled by Raunkiaer in the usual way, each with a series of 50 0.1-sq.-m. plots. For each series the effective plot-size is estimated at 0.2 sq. m.; the one-piece area equiv. to 50 plots is est. at 160 sq. m. or 35.54 mlc. The lists of spp. number 41, 47, and 78. The mean nos. of spp. per plot are 10.46, 9.78, and 12.26. The most frequent species in the 1-year græsmark are *Rumex acetosella, Lolium perenne, Anthemis arvensis, Poa annua, Alchemilla arvensis, Scleranthus annuus.* In the 8-year grassland: *Achillea millefolium, Ranunculus repens, Festuca rubra, Poa pratensis, Agrostis vulgaris.* In the Markskellene: *Festuca, Agrostis, Achillea, Galium verum, Campanula rotundifolia.*

FESTUCA RUBRA MEADOW, SAGNITZ, ESTHONIA. K. REGEL (1921). On two areas Regel established 0.25-sq.-m. quadrats, clipped and dried the herbage, separated it by species, and weighed it. His maps (Figs. 1 and 2) and tables (4 to 6) show arrangements of plots, and dry weight for each species on each plot. Two features are notable: the relatively fine texture in comparison with most other grasslands; and the considerable variability of composition from spot to spot. Regel rightly considers it a complex of many different components: he calls them associations. Most grasslands similarly are mosaics of unlike elements; to the extent that the same combination of elements is repeated over a sizable area, such a mosaic has its own degree of uniformity, and thus qualifies as an association in the American use of the term, though in fact it is an association-complex. One stand reported is on dry peat, the other on loamy soil. The two show marked difference in floristic richness, with 11.54 and 18.45 species per plot. In the stand on peat, *Festuca rubra* is strongly dominant with 62% of the total herbage. The other important species are *Salix rosmarinifolia* with 8.7%, *Stellaria glauca, Rumex acetosa, Carex vulgaris, Comarum palustre, Betula pumila, Agrostis stolonifera* 1.9%. The other area with loamy soil has only 16.5% of *Festuca rubra;* other leading species are *Phleum pratense* with 11.9%, *Poa trivialis, Poa pratensis* 8.8%, *Deschampsia caespitosa, Festuca pratensis* 5.9%, *Carex panicea* 5.0%.

Plots are systematically located: 13 in a large square in the peat area (with 1 additional larger plot), and 20 in a large rectangle in the loamy area. Regel assigns each plot to its type according to composition. Differences of composition greatly restrict the grouping of plots into aggregates for species-area treatment; only those of the same type (or of not too unlike composition) were grouped together. The ratio in an aggregate of its mean number of species per plot to the general average number per plot was applied as a correction to the apparent number of species in the aggregate. The following array shows the species-area basis for curves.

Unit or aggr., sq.m.	0.25	0.5	0.75	1.0	4.0	5.0
Equiv. 1-piece area, mlc.	0.062	0.40	.76	1.11	4.12	5.92
Spp.-no., peat	11.54	15.4	19.6	22.6	31	—
Spp.-no., loam	18.45	27	30.3	35.8	—	51

The curve for the peat area fitted the plotted points very well, the curve for the loam area only passably. For this reason the dependability-rating for loam-area results is 3 instead of 2.

PRAIRIES NEAR CRACOW, POLAND. E. MALINOWSKI (1911: 331-335). Using methods of Jaccard, Malinowski gave details for two areas of natural grassland, with 7 1-sq.-m. quadrats in each. Species occurring in all plots in the first area are: *Convolvulus arvensis, Euphorbia* sp., *Festuca elatior, Fragaria collina, Helianthemum vulgare, Medicago* sp., *Salvia pratensis, Silene nutans.* In all plots of the second example: *Equisetum* sp., *Galium Mollugo, Mentha* sp., *Poa pratensis, Ranunculus repens.* Spp. per plot: 21.4 and 15.7. In all 7 plots: 32 and 28 spp. For each example, species-numbers were also found for aggregates of 2, 3, 4, and 5 plots.

STEPPE, DISTRICT AND GOVERNMENT VORONEZH. BORIS A. KELLER (1927: 218-220). In two 100-sq.-m. areas of steppe on deep-soiled chernozem, Keller recorded 96 and 86 species. A supplementary list gives 32 additional species found in the same steppe outside the two areas. Observations were made in June, 1926. The abundant species: *Festuca sulcata, Bromus erectus, Poa pratensis* var. *angustifolia, Koeleria gracilis, Phleum Boehmeri, Carex praecox; Draba repens, Thymus Marschallianus, Filipendula hexapetala, Taraxacum vulgare, Potentilla opaciformis.* — A species-area curve was drawn, using for 100 sq. m. the mean species-number 91, and for 1 sq. m. a roughly estimated 19 spp.

AVENA DESERTORUM MEADOW STEPPE, DISTRICT OF KŪZNÉTZSK, GOVERNMENT SARATOV. KELLER (1927: 220). Abundant species: *Avena desertorum, Phleum Boehmeri, Festuca sulcata, Stipa dasyphylla, S. joannis; Anemone patens, Artemisia sericea, Filipendula hexapetala, Trifolium montanum, Achillea setacea, Inula hirta,* and *Veronica spicata.* This meadow steppe was studied in August, 1905. Keller listed 68 spp. in 460 sq. m. The est. no. of spp. at 1 sq. m. is 12.

TROPICAL SECONDARY GRASSLAND

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Cogonal, Luzon	3.58	14.5	17.6	25.1	3

COGONAL, BASE OF MT. MAQUILING, LUZON. BROWN AND MATHEWS (1914: 461). In spite of strong dominance of the tall cogon grass, *Imperata exaltata,* with 1 to 6 stalks per plant and 1976 plants in the 4-sq.-m. plot recorded, many herbs and small shrubs and vines are also present. Of these, one should mention *Desmodium pulchellum, Mimosa pudica, Selaginella Belangeri, Synedrella nodiflora, Ipomoea triloba, Merremia hastata,* and *M. umbellata. Riccia* plants are numerous. Since counts of individuals are given, it is possible to approximate the figures for smaller plot-sizes, estimating for each species the number of plots of a given size in which it will occur, from available number of plants per plot.

(The method is an outgrowth of a plot-map analysis of Brownfield Woods. From the figures obtained, graphs were made for a number of tree species over a wide range of plot-sizes, correlating the proportion of plots containing the species with the number of individuals available per plot. With the same number of plants available, proportion of plots in which the species occurs is independent of size of plot. A table prepared from the graphs gives approximate frequency of occurrence in plots for any species not showing strong tendency toward aggregation.)

Before applying this method to the cogonal, each number given for seedlings of a species was scaled down and added to those of larger plants; the number given for *"Compositae"* was apportioned among a presumed 4 different species, and *Riccia* was excluded from the list. In the detailed table made for 4 plot-sizes, there were 1976 + 329 individual plants of 19 spp. in the 4 sq. m.; 52.2 occurrences in 4 plots of the 1-sq.-m. size: thus 13.05 spp.; there were 123.9 occurrences in 16 0.25-sq.-m. plots of 7.74 spp.; and 251.3 occurrences in 64 0.0625-sq.-m. plots of 3.93 spp. — These species-numbers for the 4 sizes determined the lower part of an S-curve of rather feeble curvature, with point of flexure suggested slightly above the 4-sq.-m. plot size.

GROUND COVER OF FORESTS

There are many forms of transition between grasslands of open habitat and field-layer vegetation in shade under tree canopy. In forest ground-covers which have been studied, reference areas are considerably larger than in most grasslands. This may be a consequence of the broader leaves and more diffuse growthform of most shade-plants, in contrast to the linear or much-divided or reduced leaves of grasses and dicot herbs of the open, with usually extreme crowding of plant individuals. Because of its transitional character, and of its importance in

the development of species-area studies, Gleason's vegetation of the open parts of burnt-over pine lands in Michigan is first examined. Since the large-toothed aspen, *Populus grandidentata,* is the common tree in the sandy soils of these former pine forests, such tracts are spoken of as the aspen association or "the aspens," but the open parts are treeless over various-sized areas up to several acres. Aspens may be thinly scattered in these open parts; in other places small groups or fair-sized groves or stands of aspens occur, usually with some other tree species which soon follow. Thus there are two kinds of vegetation, actual young forest, and a herb–dwarf-shrub ground cover which has elements of grassland, of dwarf shrub, and of open-forest undergrowth. Probably only young forest should be called "aspen association." It is the herb–dwarf-shrub cover, dominated in most parts by *Vaccinium pennsylvanicum* and *Pteridium aquilinum,* in which Gleason's studies were made. The first data were published in 1920, species-area results from the same data in 1922, and additional results from new data in 1925.

TABLE 18. Bracken—Blueberry Ground-Cover, Michigan.

Stand	Am, *mlr*	Am, *sq. m.*	Sr	Sm	D
Area of earlier study (1922)	57.5	232.5	17.7	26.6	1
Series 1, Tract 1 (1925)	47.7	193.0	20.3	30.3	3
Tract 2	49.6	200.6	21.2	31.6	3
Series 2, Tract 4	62.4	252.1	35.4	50.6	3
Tract 5	59.4	236.1	27.6	39.7	3
Tract 6	49.0	198.1	33.0	47.4	3
Tract 7	67.2	271.3	32.0	46.0	3
Tract 8	73.7	298.0	34.8	49.6	3

BRACKEN–BLUEBERRY GROUND-COVER AMONG ASPENS, NORTHERN LOWER MICHIGAN. H. A. GLEASON (1920, 1922, 1925). Most of Gleason's studies were made near Douglas Lake, not far from the north end of the lower peninsula. Each tract consists of a considerable number of 1-sq.-m. quadrats. The 1920-22 data cover 240 such plots, with 27 spp. Mean no. of spp. per plot is 4.375. Each of these species-numbers is for a single compact area. For intermediate plot-sizes: 4-sq.-m. plot-groups average 7.60 spp.; 16-sq.-m. size, 12.0 spp.; 60-sq.-m. size, 19.75 spp. These intermediate-sized areas are contiguous quadrats in a row, and are less compact in form as the number of quadrats increases.

Gleason's species-area graph had a rather small vertical scale for number of species, and its configuration of points shows rather small departures from those which a straight line would fit. This is the earliest graph known to the writer in which mean number of species is plotted against logarithm of area. (O. Arrhenius had developed a formula, published in 1920, for which the graphic analogue is a plotting of logarithm of species-number against logarithm of area. Du Rietz's "Methodologische Grundlage" includes graphs so constructed for seven communities in Sweden [1921: Figs. 18, 19; pp. 205-206]. These graphs

show lack of agreement with Arrhenius' formula. Du Rietz put greater stress on his other graphs showing number of *constant* species plotted against area, and against log area, as well as log number of constants plotted against log area.) Gleason inferred from his graph that species-number is directly proportional to logarithm of area. Later he came to realize that the relation is not so simple as to be represented by a straight-line graph.

It is of interest, in view of the much later finding that the usual species-area graph on semilog paper is S-shaped, to reexamine the graph published by
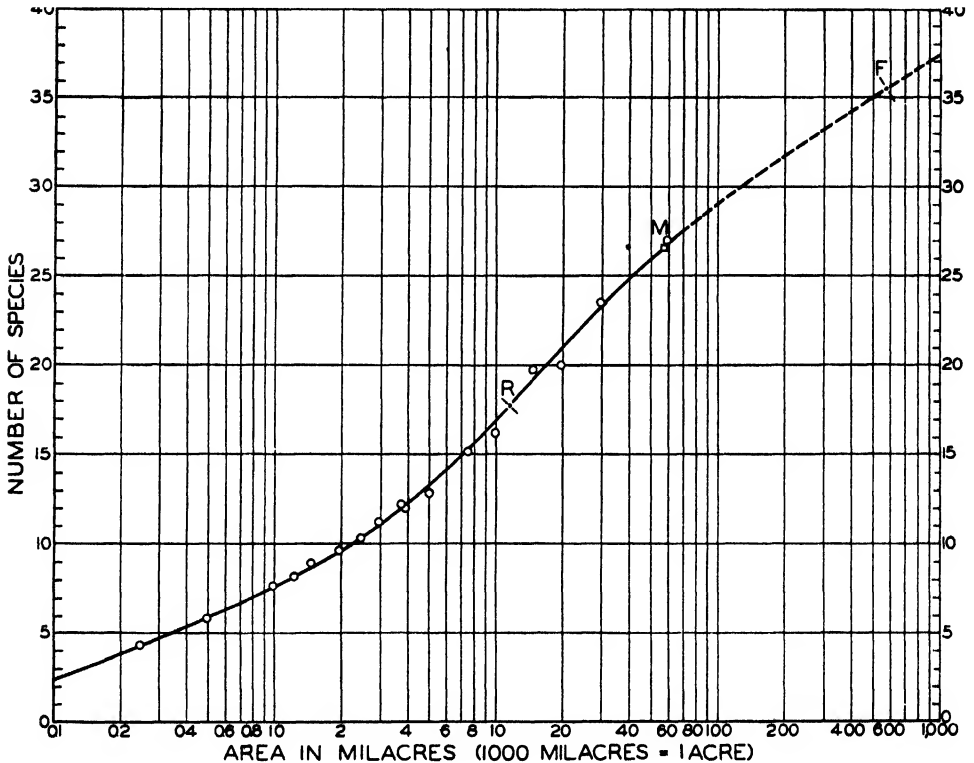
FIGURE 4. Gleason's species-area graph of 1922 for bracken–blueberry ground-cover in Michigan, redrawn as a smoothed S-curve. The original was the first graph of this type, so far as the writer is aware. Minimum area is 57.5 milacres, with 26.6 species. This growth of herbs and low woody plants covers the mostly treeless parts of sandy aspen lands.

Gleason in 1922 (his p. 161). The S form is evident, the lower part of the curve being concave, the upper part slightly convex. Gleason's figure is thus the first graph of the type adopted in this study 22 years later. When Gleason's graph is redrawn as a smoothed S-curve (Figure 4), it is seen that the fit is good.

In Gleason's publication of 1925, figures are given for 7 additional locations in the aspens, in two series, Tracts 1-2 and Tracts 4-8. Although an adequate number of points was available for the 1922 curve, plot-sizes for some tracts in the 1925 article were few, and the sizes intermediate between smallest and

largest were aggregates of well-scattered plots, rather than single compact areas. An adjustment comparable to an I-conversion, to find numbers of species in a one-piece area of the same total extent, was therefore necessary.

Tracts 1 and 2 had 3 intermediate sizes: 4, 16, and 64 sq. m., while Tracts 4 to 8 had only one: 100 sq. m. Curves for Tracts 1 and 2 were made by plotting the given points on the same sheet as the 1922 curve, and patterning the form of the new curves after that of the old one. For the others, the S-curve for Tract 1 was compared with a graph made to fit the non-adjusted Tract-1 values. From this graph, the species-number for 100 scattered quadrats was found to be 27.46; from the S-curve the approximate value for a 100-sq.-m. compact area was found to be 26.43. The rather slight reduction in number of species at this plot-size was the chief means of estimating the adjusted S-values for Tracts 4 to 8. The whole array of given values and adjusted values may be seen in the accompanying table, in which A represents area in square meters, S represents number of species. For Tracts 1 and 2, those S-values which were read from the graphs are shown in parentheses.

TABLE 18a. Species-Area Data for Bracken—Blueberry.

Tract	S at 1 sq. m	A	Intermediate areas: Given S	Intermediate areas: Adjusted S	Largest area: A	Largest area: S
1	4.82	16	17.38	(14.82)	256	32
		64	25	(23.72)		
		100	(27.46)	(26.43)		
2	4.88	16	19.0	(15.07)	256	33
		64	28.0	(24.31)		
4	4.19	100	44	41.85	8492	84
5	4.62	100	34	33.0	4350	59
6	4.75	100	44	41.5	8895	77
7	4.15	100	39	37.5	6142	70
8	4.15	100	41	39.5	44331	91

HERBACEOUS GROUND COVER UNDER FOREST

The first group of these herbaceous ground-cover communities under fairly dense tree canopies comprises four forests in Michigan of aspen-birch and beech-maple types (Table 19). It is presumed that tree seedlings are included in the counts for some of these and of other forest field layers. Also in Table 19 are beech forests and oak forests in Europe. Two very different types are appended: herbaceous field layer under spruce in Denmark, and a relict sand-prairie vegetation under more or less open blackjack oak in the Illinois River dunes.

TABLE 19. Herbaceous Ground-Cover under Forest.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Aspen–birch, Michigan: Tract 3	73.8	298.3	21.2	31.7	3
Beech–maple, Emmet Co.: Tract 9	68.4	276.8	14.9	22.1	3
Beech–maple, Antrim Co.: Tract 10	65.8	266.2	23.1	34.4	3
Beech–maple, s.w. Michigan	75.8	306.9	21.5	31.7	3+

TABLE 19 (*continued*). Herbaceous Ground-Cover under Forest.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Beech, Gribskov	79.3	320.5	17.0	24.7	3
Beech, Farum Lillevang	48.8	197.7	19.2	28.4	3
Beech, Jonstrup Vang	116	469.2	12.1	17.9	3
Oak, Jonstrup Vang	43.1	174.4	29.8	43.4	3
Spruce, Egebjergene	81.7	330.8	14.3	20.9	3
Quercus marilandica, Illinois	163	660.0	16.0	24.0	2

GROUND-COVER UNDER ASPEN AND BIRCH, MICHIGAN. GLEASON (1925:67). This was studied "in a dense grove of *Populus* and *Betula,* with the ground heavily shaded and with some accumulation of leaf mold." It contrasts with bracken–blueberry cover of open areas within the aspen lands already described. This shaded undergrowth is listed as Tract 3 of Series 1, and like Tracts 1 and 2, comprises 256 1-sq.-m. quadrats, with species-numbers for 1, 4, 16, 64, and 256 plots: intermediate sizes are aggregates of scattered plots. Spp. per plot, 3.06; in 256 plots, 31. For the 64-plot aggregate, 22.75 spp. Reduced species-number for compact single area of 64 sq. m., 21.3.

GROUND-COVER UNDER BEECH–MAPLE FORESTS, MICHIGAN. SERIES 2, TRACTS 9 AND 10. GLEASON (1925). Tract 9 comprises 2500 sq. m. in a 40-acre stand in Emmet Co. Tract 10 covers 6400 sq. m. in a remnant of 100 sq. miles of forest in Antrim Co. They were recorded in the same manner as bracken–blueberry Tracts 4 to 8, and curves were made from the data as for Tracts 4 to 8. The species-numbers are:

Tract	For 1 sq. m.	For 100 scattered plots	For 1 plot of 100 sq. m.	For whole tract
9	2.93	19	17.65	32
10	3.73	30	28	46

GROUND-COVER UNDER BEECH–MAPLE FOREST, SOUTHWESTERN MICHIGAN. L. F. KENOYER (1927:344). The extremely condensed data give the number of species in each of 5 frequency classes (20% steps), in 25 quadrats, each of 10 sq. m. From these figures a distribution was made, showing the likely number of plots in which each of the 37 species occurs. Thus for the highest class, 81 to 100%, 1 of the 2 species was assumed to occur in 25 plots, the other in 23. The total number of occurrences per plot was estimated to be 202, making 8.08 species per plot. This may be somewhat too high. Since the plots were separated, fewer than 37 species would occur in a compact 250 sq. m. plot. The reduced number for this size was estimated at 30.5. Such a curve, based on two points, is of only suggestive value; it gives reference areas somewhat larger than those for Gleason's three stands. Superposed on the graph for these forests, it nearly coincides with the curve for Tract 3, aspen–birch, but has slightly steeper gradient.

GROUND-COVER UNDER BEECH FOREST, GRIBSKOV, DENMARK. 4 LOCATIONS. M. VAHL (1911: 334, TABLE 2). The table summarizes occurrence in 50 0.1 sq. m. plots of 5 woody and 35 herbaceous species in each of 7 stations, 5 being in the forest known as Gribskov, or Grib Skov, not far from Copenhagen. Omitting station D (less rich in species), and eliminating tree and shrub species, the following data apply to the four Gribskov stations A, B, C, and G, in order. Spp. per plot: 4.7, 4.48, 6.06, 4.78. Spp. in 50 plots: 12, 14, 17, 14. In the 4 series of plots: 34 spp. For the composite of four series: 5.01 spp. per plot, 14.25 spp. in 50 plots. Estimate of effective plot-size, 0.3 sq. m. One-piece area equiv. to 50 scattered plots: 28.8 to 48 sq. m. One-piece area large enough to include 34 spp., 2400 to 4500 sq. m. Minimum areas for similar stations would presumably range from 60 to 100 milacres. One reason for their considerable extent is that much of the area is occupied by tree seedlings, saplings, or shrubs. Also, as in many other forests, heavily shaded parts may have only a few individuals of the few species that can endure both heavy shade and the smothering effect of repeated falls of dead leaves from the tree-crowns above. — In Gribskov, *Fraxinus excelsior* is a moderately frequent companion of *Fagus silvatica*. Herbs of high frequency in at least two of the four stations are *Anemone nemorosa, Asperula odorata, Oxalis acetosella, Mercurialis perennis* and *Milium effusum*. Frequent in individual stations are *Equisetum silvaticum* in A; *Maianthemum, Convallaria, Trientalis,* and *Poa nemoralis* in B; *Stellaria holostea* and *Viola silvatica* in C; and no distinctive species in G.

BEECH UNDERGROWTH, FARUM LILLEVANG, AND JONSTRUP VANG (NOT FAR FROM COPENHAGEN). RAUNKIAER (1910: 60-64). These are 2 of 7 beech ground-covers summarized in Raunkiaer's Table 15. Herbs only are included in these series of 50 0.1-sq.-m. plots. Spp. per plot and spp. in 50 plots for these 7 stations are: No. 1, Jonstrup Vang, 1.60 and 12; 2. Nørreskov, 3.4 and 15; 3. Lille Hareskov, 3.08 and 8; 4. Valløskov I, 3.8 and 10; 5. Vall skov II, 4.4 and 12; 6. Farum Lillevang (the richest in spp.), 6.22 and 20; 7. Bognæs (the poorest), 1.22 and 6. In the last, *Allium ursinum* is dominant. At Farum Lillevang, *Anemone nemorosa, Milium effusum, Oxalis, Asperula, Viola silvatica* and *Melica uniflora* occur in 50 to 29 plots. At Jonstrup Vang, only *A. nemorosa* is dominant (in 50 plots). *Oxalis* is in 8 plots, *Melica* in 3. In a more detailed table for the *Anemone nemorosa* facies on p. 29, Raunkiaer lists in 100 0.1-sq.-m. plots, only 7 spp. which occur in more than 1 plot. Aside from the dominant *Anemone, Gagea lutea* is in 17 plots, *Oxalis* in 16. Plot-numbers for the next 4 spp. are 5, 4, 3, and 2. — The curve for Lillevang was made in the manner described for Vahl's Gribskov ground-cover. For Jonstrup Vang the detailed table gave independent data for 4 plot-sizes: 0.01, 0.1, 1.0, and 10 sq. m. The species-area curve gave the Am-value of 116 mlc. This large minimum area is attributed to the pronounced dominance of *Anemone,* which leaves so little room for other herbs that a large surface must be surveyed.

OAK UNDERGROWTH, JONSTRUP VANG. RAUNKIAER (1910: 57-60). 4 locations near Jonstrup Vang are given in 4 columns of Raunkiaer's Table 13. Number 4, considered most nearly representative, is west of the place known as Maal$_\emptyset$vmose. The herb cover is named *Convallaria majalis–Aira flexuosa* facies. The most frequent plants are *Convallaria, Aira, Anemone, Maianthemum,* and *Viola silvatica.* There are 34 spp. in the 50 0.1-sq.-m. plots. Spp. per plot, 6.04. Estimated one-piece area equivalent to 50 plots, 34.6 sq. m., = 14 mlc. If curve and computations are approximately correct, this herb cover under oak has smaller reference areas (Am is 43.1 mlc.) than any of the 16 other forest undergrowths of Tables 19 and 20.

OXALIS ACETOSELLA FACIES UNDER PICEA EXCELSA, EGEBJERGENE, NEAR JONSTRUP VANG. RAUNKIAER (1910: 70-75). In four 50-plot series, Raunkiaer gives data for *Aira flexuosa* facies with 8 spp., *Aira–Oxalis* facies with 9 spp., and two examples of *Oxalis* facies, with 6 and 10 spp. The last was made the basis of a curve. The location is in a *Granskov* near a beech forest bordering its southern part. Spp. per plot, 1.34. Estimate of one-piece area including 10 spp., 15 sq. m. or 6.18 mlc.

SAND-PRAIRIE GROUND-COVER UNDER BLACKJACK OAK, ILLINOIS RIVER DUNES. GLEASON (1907: 175, TABLE 10). Most stands of the xeric *Quercus marilandica* are young, the shade and leaf-litter are not heavy and the sand-prairie vegetation present before invasion of the trees is still the only ground-cover. The same is true of young stands of black oak, *Q. velutina,* in the dunes. There is also an older dune forest of mixed composition in the river dunes adjoining the east bluff of the Illinois River, with true forest-herb undergrowth, but an almost complete change of ground flora takes place in its development. In the xeric young forest away from the river, the ground flora is practically identical with that of treeless areas, with higher frequency and greater abundance of a few species, notably *Tephrosia virginiana,* a legume with handsome pea flowers, and the poppy mallow, *Callirrhoë triangulata.* Gleason's strip of 17 plots, each 10 × 10 ft., does not include *Callirrhoë.* 12 plots are in a brushy part of a blackjack stand, 5 are in a more open part. Since the most frequent species are the same in both parts, they are here treated as a unit. These most frequent species are: *Tephrosia, Opuntia humifusa, Aristida tuberculosa, Euphorbia corollata, Teucrium canadense,* and a bushy shrub, the sand form of *Rhus aromatica.* This last is not part of the herb cover, but is everywhere at home in sand prairie, as thinly scattered bushes, or forming clumps or extensive low shrubberies. (It is an effective sand-binder and dune-former: an important component in the vegetation complex of the dunes.) — Gleason's 17 plots include 18 spp. Spp. per plot, 5.88. Recombinations of plots gave data for 5 intermediate plot-sizes. The compact area equivalent to the 17-plot strip is est. at 46.8 milacres. Reference areas are larger than for true forest ground-covers, or for sand prairie. *Tephrosia* and *Rhus* occupy much space; most other species are thinly scattered.

DWARF-SHRUB GROUND COVER OF BOREAL FORESTS

North European plant geographers have recorded many examples of field-layer vegetation under trees or in the open parts of scattered-tree stands. Birch, Scots pine, spruce, and juniper are the common tree species. Dwarf shrubs are the usual dominants. With them are seedlings and stunted individuals of the trees, herbs of many types, including *Lycopodium* and true-fern species, grasses, sedges, and wood-rushes. Mosses and lichens, though frequently listed or mentioned, are not included in the present counts. The tall-shrub and tree species when listed are taken to be part of the field layer, and are included in the counts. It is not usual to find an explicit statement whether small plants of these larger species are or are not part of the field layer.

TABLE 20. Boreal Dwarf-Shrub Ground Cover Under or Among Trees.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Vaccinium—birch, Island Jungfrun	59.3	240.0	12.6	18.6	3
V. vitis-idaea—pine, Järvis, Finland	57.6	233.1 ·	17.4	25.2	3
V. vitis-idaea—pine, Hillilä, Finland	62.2	251.4	18.9	27.5	3
Vaccinium—pine, Järvis, Finland	66.5	269.0	21.5	32.0	3
V. myrtillus—pine, Kola peninsula	107.0	433.1	12.3	18.3	3
V. myrtillus—pine, Island Sandön	95.2	385.0	13.1	19.5	3
Same, pines excluded from count	110.5	446.8	12.8	19.0	3
Calluna—pine, Island Sandön	49.0	198.3	5.64	8.16	3

VACCINIUM AND OTHER DWARF-SHRUBS UNDER BIRCH, ISLAND JUNGFRUN. DU RIETZ (1921: 148). (NACKTER PREISELBEERBIRKENWALD.) Jungfrun is about 20 km. east of the mainland of southern Sweden in lat. 57° 15′; it is in the northern opening of Kalmar Sound, about 8 km. west of the long island Öland. Du Rietz specifically lists each larger species in each of the layers in which it occurs. *Betula alba, Juniperus communis, Q. robur, Rhamnus frangula,* and *Sorbus aucuparia* are in the field layer. *V. vitis-idaea* is dominant, though *V. myrtillus* is likewise present in all plots recorded (44 of 1 sq. m., 10 of 4 sq. m.). *Calluna* and *Empetrum; Melampyrum, Deschampsia flexuosa,* and *Pteridium,* are notable. Mosses and lichens are infrequent. — Effective small-plot size is 0.3 mlc., with 5.38 spp.; for the larger plots 1.06 mlc. with 7.9 spp.; 15 spp. in 21.1 mlc.

VACCINIUM VITIS-IDEA–PINE, JÄRVIS IN PARISH OF NASTOLA, FINLAND. K. LINKOLA (1922: 16-21). Linkola studied in July, 1917, 7 stands of *Vaccinium* under pine. This locality, no. 4, is a moderately steep north slope with 50-year pines. The plot, taken to be 15 meters square (55.6 mlc.), has 2 conifers, 2 dicot tree spp., 2 dwarf shrubs (no *V. myrtillus*), 15 dicot herbs, 5 grasslike herbs, 3 other monocot herbs, 3 mosses, 1 lichen. At least 25 spp. are in the field layer. Curves for this and 2 others of Linkola's stands were made possible by the presumed similarity in form to the curve for Du Rietz's Heidelbeerkiefernwald.

V. VITIS-IDAEA–PINE, NO. 6, HILLILÄ IN ASIKKALA PARISH. LINKOLA (1922).
A few plants of *V. myrtillus* are in the no. 6 plot, which has 25- to 75-year-old
pines, and is at the foot of a ridge. It is somewhat richer in composition, with
4 dwarf-shrub spp. and *Pteridium*. At least 27 field-layer spp. are in the plot.

VACCINIUM–PINE, NO. 3, JÄRVIS. LINKOLA (1922). On flat top of a ridge
(Åshügel). 10- to 70-year-old pines. 3 dwarf-shrubs, 20 dicot herb spp., 6
grasslike herbs, no lichens. *V. myrtillus* and *V. vitis-idaea* equally abundant.
37 spp. in all, at least 31 in the field-layer on the plot.

V. MYRTILLUS–PINE, KOLA PENINSULA. K. REGEL (1923: 65). (Aufnahme
No. 20, in Pinetum myrtillosum, July, 1913). Plot is 10 × 10 steps, taken to
approximate 9 × 9 meters (870 sq. ft., or 19.93 mlc.). *Pinus lapponica* and
Picea excelsa; V. myrtillus, V. vitis-idaea, Empetrum, Calluna, Ledum palustre.
Several herb spp., including *Lycopodium annotinum*. No grasses; 2 moss spp.
Including the 2 trees, 12 spp. are in field layer of the plot. Curve is patterned
after that of Du Rietz, which follows.

V. MYRTILLUS–PINE, ISLAND SANDÖN. DU RIETZ (1921: 149-153). (Moos-
REICHER HEIDELBEERKIEFERNWALD.) Sandön is in the Stockholm Skärgård
close to the east-Swedish coast. It is about 35 km. east of Stockholm. The only
tree is *P. silvestris*. The 5 dwarf-shrubs are *Vaccinium* (2 spp.), *Calluna,
Empetrum, Arctostaphylos uva-ursi*. As in the case of one or two dwarf-shrub
heaths, (treated in an earlier section), Du Rietz presents a detailed summary
for 6 plot-sizes; 1000 plots of 0.01 sq. m., 250 of .04, 40 of the .25-size, 330
quadrats of 1 sq. m.; 80 of 4 sq. m., and 20 of 16 sq. m. Effective plot-sizes and
one-piece areas equivalent to the different aggregates were estimated. Species-
numbers ranged from 2.67 at the effective size of .03 mlc. to 20 at 127.7 mlc.
These numbers include the pine. A curve was drawn for this array, and a second
curve for the same plot-sizes omitting the pine. The difference in results may
be seen in Table 20. When the tree species is excluded, considerably larger
reference areas are required.

CALLUNA–PINE, SANDÖN. DU RIETZ (1921: 153). (FLECHTENREICHER
CALLUNAKIEFERNWALD). This combination is extensive on sandy soils in
various parts of Sweden, and elsewhere. *Calluna* and *V. vitis-idaea* are the chief
constants, with *P. silvestris. Arctostaphylos, V. myrtillus,* and *Empetrum* are
the other dwarf-shrubs. *Melampyrum* and *Festuca ovina* are present. *Cladonia
rdngiferina* covers much of the ground surface. Although Du Rietz does not
list small pines as part of the field layer, trees are indicated as present in or cover-
ing all of the 4-sq.-m. and 16-sq.-m. plots. Arbitrarily estimated frequencies for
the 4 smaller plot-sizes have been added to his table in order to compute species-
numbers. Only 8 spp., including pine but no lichens or mosses, are given in the
table. Species-numbers range from 1.62 for the .01-sq.-m. size (effective area
.03 mlc.) to 8 spp. at an estimated 44.2 mlc. This heath-forest ground-cover

has smaller reference areas than any others composed chiefly of dwarf-shrubs. There is more reason to exclude pine from the count for this heath forest than from the *V. myrtillus* ground-cover. If this were done, the reference areas would probably still be no larger than in any of the other dwarf-shrub covers.

The reader may find some interest in comparing these field-layer communities under or among trees with their equivalents in treeless areas, as previously included in Table 10 (heath and dwarf-shrub): Am-values 21.3 to 61.7 (two extreme types omitted). The generally larger reference areas in forested country are expectable: tree-trunks, dense groups of young conifers, heavily-shaded spots, etc., make numerous breaks in the field layer. — Certain similarities to the bracken–blueberry ground-cover in Michigan could be suggested. Ranges of minimum areas are: 47.7 to 73.7 mlc. for bracken–blueberry; 49 to 110.5 mlc. for the more diverse European types of Table 20. Species-numbers are generally higher in bracken–blueberry.

One more forest ground-cover study must be reported. T. A. NOSKOVA published in 1928 an article in Russian on minimal-area in forest associations. The original has not been seen, but the summary by G. A. LEBEDEFF in BIOLOGICAL ABSTRACTS (ENTRY 21350 IN VOLUME 6) is useful. Minimal area is defined as the smallest plot of land on which all of the peculiarities of a given plant association are developed. For three types of forest the minimal area was found to be 500 sq. m. (123.6 mlc.). These types are PINUS–PTERIDIUM–HYLOCOMIUM, PINUS–QUERCUS–TILIA, and PINUS–QUERCUS–PTERIDIUM. For the PINUS–CLADINA type it is 400 sq. m. (98.8 mlc.). If, as is likely, the tree species in any one stand are few, the minimum area for trees may be no larger than that given for plants of the ground layer. The minimal areas given for these Russian forests are in a size range which overlaps the larger Am values for the northwest-European forests in Table 20.

GROUND VEGETATION WITHIN TROPICAL FORESTS

The only examples used for ground-cover in tropical forests are those of J. G. B. Beumée (1922) for stands of teak (*Tectona*) in Java. The original publication was not available; data were taken from the compact summary by O. ARRHENIUS (1923: 69, TABLE 3). This does not include descriptions, but considerable information is provided in MARKGRAF'S abstract.

TABLE 21. Herb and Lower Woody Vegetation, Teak Forests, Java.

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Beumée's No. 16a	910	3677	41.1	61.9	2
23b	797	3223	13.8	20.9	3
23a	712	2878	14.8	22.3	3
26	705	2851	50.8	76.0	2
21a	680	2751	32.1	47.3	3
33	660	2667	42.3	61.6	3
18	484	1959	75.3	111.1	2

GROUND OR LOWEST-STORY VEGETATION IN TEAK FORESTS, JAVA. BEUMÉE (1922). It seems likely from descriptions of other tropical forests that the undergrowth is very different from that of most temperate forests. There are fewer and much larger herbs, few or no rounded or flat-topped shrubs, but in their place, crowds of slender arbuscules of many species and of varying height. Large-tree species are usually represented by varying numbers of seedlings and young trees. There may also be course grasses, especially in disturbed areas. Understories in Beumée's stands evidently differ widely, in floristic richness and in rate of increase of species with area, as shown by greatly differing steepness of the curves. The number of given plot-sizes varies from 4 to 7. Largest plot-size (with 39 spp.), is 1400 sq. m. (locality 21a). For 3 other stands the largest plot-size is 1200 sq. m., with 49.5 to 103.7 spp. Smallest plot-size is in all 7 instances 100 sq. m., with species-numbers from 4.5 in No. 23b to 40 in No. 18. No. 23b has only 16.7 spp. at the largest size given, 1000 sq. m. The steepest curve, that of No. 18, suggests that a high rate of species-increase continues into much larger areas than in temperate forests: i.e., the supply of additional species available within the district and able to enter into the mixture is perhaps 5 to 10 times as great as in a floristically rich temperate-forest district. Because of this continued rate of species-increase (and of the greater size of the plants), reference areas of No. 18 are larger than in ground-covers of any temperate-forest examples studied. The largest Am value in Tables 18-20 is 116 mlc. (if we exclude the somewhat aberrant ground vegetation under blackjack oak, 163 mlc.). This compares with 484 mlc. for teak stand No. 18.

The other teak stands have even larger reference areas, but not as the probable consequence of their having many species, nor from persistent rate of species-increase. More information is required for these stands. It may be added that the Am values in Table 21 are conservative, and that fuller information might give considerably larger areas. For example, if the S-curve for No. 18 is made to fit the points exactly (it is possible in this case), the resulting Am is 662 mlc., with correlated Sm of 121 species.

Markgraf notes: "Wenn man nun feststellt, wieviel Prozent aller Arten den Probequadraten eines Bestandes gemeinsam sind (nach Jaccard), so erhält man erst für die 4000-qm-Flächen einen Wert, der dem von Jaccard für 1-qm-Flächen in europäischen Wiesen gefundenen nahekommt. . . ."

BOG VEGETATION

Results for nine sets of data on bog communities are shown in Table 22. Four of them are dominated by dwarf-shrubs; in the second group of four, sedges are dominant, although *Vaccinium oxycoccus* (cranberry) is abundant in some of them. The ninth enumeration includes only bryophytes. These nine examples are treated as one-layered communities; differentiated results for field and moss layers are given, in a later section on vegetation of mixed growth-forms, for some three-layered raised-bog communities described by N. and S. Katz (1926).

TABLE 22. Bog Communities.

Stand or type	Am, mlc.	Am, sq. m.	Sr	Sm	D
Ledum—Sphagnum, near Torneträsk	0.077	0.291	5.35	8.01	3
Empetrum—Calluna, Sækkedammen	0.215	0.870	2.26	3.33	3
Empetrum—Calluna, Lyngby Moss	0.625	2.53	4.90	7.17	3
Chamaedaphne bog near Kalamazoo	10.6	42.9	15.1	21.9	3
Sphagnum moor, Maaløv Krat	1.162	4.70	8.71	12.6	3
Carex—Sphagnum, Maaløv Krat	1.536	6.22	9.07	13.1	3
Eriophorum—Oxycoccus, Maaløv Krat	1.774	7.18	10.4	15.1	3
Carex lasiocarpa bog, northern Mich.	100.0	404.7	12.3	18.8	2
Sphagnum—Hylocomium—Hypnum, Maglemose	5.00	20.2	9.43	14.3	2

LEDUM PALUSTRE–SPHAGNUM FUSCUM HOCHMOOR, NEAR TORNETRÄSK STATION, EASTERN LAPLAND. DU RIETZ (1921: 162, TABLE 17). The type is extensive in Lapland. Du Rietz gives data for field layer only, listing 12 spp. in 40 1-sq.-m. quadrats, and in 10 4-sq.-m. quadrats. In every square meter occur *Ledum, Empetrum, Andromeda polifolia, Vaccinium vitis-idaea, V. microcarpum, Betula nana,* and *Rubus chamaemorus. V. uliginosum* and *Pinguicula villosa* are also frequent. Spp. per 1-sq.-m. plot, 9.825; per 4-sq.-m. plot, 10.7; 12 spp. in est. one-piece area of 13.9 mlc. The configuration of plotted points indicates that the species-area curve is already in its convex upper section at 1 sq. m. Extension of the curve leftward results in the extremely small Am value 0.077 mlc., which is only 29.13 sq. dm., or 3.35 sq. ft. If this is not a mistaken value, a "complete stand" (Am $\times$ 20) could be exhibited in a garden plot or museum case 11 feet long by just over 6 feet wide.

EMPETRUM–CALLUNA BOG: SAEKKEDAMMEN, A MOSS IN RUDER HEGN, DENMARK. RAUNKIAER (1910: 83). The location is about 10 miles n.n.w. of Copenhagen. Only 5 species of vascular plants are listed in the 50 0.1-sq.-m. plots of this enumeration. *Empetrum* occurs in all 50, *Eriophorum vaginatum* in 38, *Calluna* in 27, cranberry (*Oxycoccus palustris*) in 21, and *V. uliginosum* in 2. — "Effective plot-size" is estimated at .0875 mlc., with 2.76 spp. per plot. One-piece equivalent of the aggregate is 7.5 mlc. The Am value is about 3 times that of the preceding community.

EMPETRUM–CALLUNA BOG: LYNGBY MOSS, DENMARK. RAUNKIAER (1910: 83). Lyngby is not far n.n.w. from Copenhagen. *Empetrum* is in 47 plots of this enumeration, *Eriophorum* and cranberry each in 48, *Calluna* in 30. *Drosera, Menyanthes,* 3 species of *Carex* in a few plots, and *Scheuchzeria* in 2 plots, complete the list. Spp. per plot, 4.42. Effective plot-size and one-piece equivalent area are as in Sækkedammen.

CHAMAEDAPHNE BOG NEAR KALAMAZOO, S.W. MICHIGAN. L. A. KENOYER (1927: 347). This is the low-shrub zone of a typical peat bog of the vicinity. The survey comprises 25 1-sq.-m. quadrats in line, separated by 4-pace intervals.

It includes density estimates as well as frequency of occurrence in plots. *Sphagnum* sp. is listed as in 23 plots, *Aulacomnium palustre* in 16; these mosses were not omitted from the species-area treatment. *Chamaedaphne calyculata,* the dominant, is in all plots, with 1320 individuals. Herbs of diverse types include a *Sagittaria,* a grass, a rush, 2 *Carices,* the orchid with grasslike leaves *Calopogon pulchellus, Drosera,* a violet, and *Menyanthes. Vaccinium macrocarpum* is in 9 plots, *Solidago* sp. in 12, *Aspidium thelypteris* in 8. The total estimate of individuals is 3242, about 130 plants per sq. m. Spp. per plot average 6.08. Spp. in the 25 plots, 22. Estimated one-piece area is 11.0 mlc. The vegetation is apparently less homogeneous than the north-European bogs. The larger number of species is partly due to the larger area surveyed (5 times the usual Raunkiaer aggregate).

SPHAGNUM MOOR, MAALØV KRAT, DENMARK. RAUNKIAER (1910: 81, 83, TABLE 25, COLUMN 3). Raunkiaer studied bogs of a moor-complex in the Maaløv Krat district south of the west end of Jonstrup Vang (Meadow). These places are also n.n.w. of Copenhagen. The terrain is a high upland dotted with ponds, many of which are excavations for peat. This enumeration is for a quite small *Sphagnum* moor just west of Haven. It is assigned to the *Eriophorum–Oxycoccus* facies. In its highest part are a little *Polytrichum* and *Calluna;* in the surrounding narrow zone are *Hypnaceae* with *Equisetum* and *Carices* but no *Sphagnum* or *Eriophorum.* — The main bog area has cranberry in 41 plots, *Eriophorum vaginatum* in 48, *E. polystachyum* in 23, *Carex stricta* in 26, *C. rostrata* in 23. In all 50 plots are 16 spp. Mean no. of spp. per plot, 5.46. One-piece area equivalent to aggregate is 5.36 mlc.

CAREX–SPHAGNUM MOOR, MAALØV KRAT. RAUNKIAER (1910: 80, 83, TABLE 25, COLUMN 1). This and the next example are parts of a bog which, with two nearby bog areas, is located near the road between Blide and the Ballerup-Jonstrup road. This bog has an upper and a lower border zone, an open-water zone with *Menyanthes,* around the principal raised-bog area designated *Sphagnum* Hængesæk. This itself has three parts: a quaking outer zone, a firmer part in which 50 plots were studied, and the middlemost, somewhat higher part forming the next example. The firm part around the middle is characterized by a combination of 4 species: *C. rostrata, C. canescens, Agrostis canina,* and *Oxycoccus palustris.* They occur in 50, 36, 39, and 49 plots. The only other species of fairly high frequency is *Peucedanum palustre* in 25 plots. There are 16 spp.; 5.08 per plot.

ERIOPHORUM–OXYCOCCUS FACIES, MAAL V KRAT. RAUNKIAER (1910: 81, 83, TABLE 25, COLUMN 2). This enumeration is in the high central part of the Hængesæk just described. It is assigned to the same facies as that of the *Sphagnum* moor just west of Haven. Of 4 leading species, *Oxycoccus* is in 49 plots, *E. vaginatum* in 46, *E. polystachyum* in 37, and *Carex rostrata* in 36.

Drosera occurs in 24 plots, *Scheuchzeria palustris* in 15, *Andromeda* in 14. There are 18 spp. in all; 5.60 per plot. Equivalent area and effective plot-size are the same in all three Maaløv Krat examples: 5.36 and 0.0618 milacres. This is the richest in species of the European bogs treated.

CAREX LASIOCARPA BOG, CHEBOYGAN COUNTY, MICHIGAN. EDITH WOOL-LETT, DORIS DEAN, AND HELEN COBURN (1925). The authors studied species and area in Smith Bog in the north part of the Lower Peninsula, not far from Douglas Lake. A nearly uniform mat of the dominant sedge covered 23,159 sq. m. (5723 mlc.). Double rows of contiguous 1-sq.-m. quadrats were arranged along lines wholly within the *Carex* area. There were 1050 plots (259.6 mlc.). The entire area was searched for species not in the plots, making a total of 29 species. 21 occurred in the plots; mean no. of spp. per plot was 2.65. No other species approached the dominant in frequency (it occurred in all 1050 plots). Some of the others are: *Dulichium arundinaceum* in 390 plots, *Eleocharis palustris* in 380, *Potamogeton heterophyllus* in 240, *E. acuminata* 207, *Juncus crinita* 94, *Lysimachia terrestris* 61, *Potentilla palustris* 51, *Chamaedaphne calyculata* 50. — One-piece area equivalent to the plots was estimated at 285 mlc. There were thus 3 widely separated points through which an S-curve was drawn. The large reference areas resulting are attributed to strong domination by *C. lasiocarpa* and to the persistence into very large areas of about the same rate of addition of species. This rate, though low, continues over the graph in a nearly straight line; it almost maintains a logarithmic rate. This has the effect of determining higher positions on the curve of the two points Ar and Af (smallest and largest of the 3 reference areas).

MAGLEMOSE, NEAR GRIB SKOV, NORTHERN ZEALAND, DENMARK. CARSTEN OLSEN (1920). Bryophyte vegetation is presented in detail for 5 groups of 36 0.1-sq.-m. plots; in another set of 121 plots, 6 species of *Sphagnum* are the only plants listed. — Olsen's article is the fifth part of a series of papers on Maglemose; the preceding parts were published together in 1919 in the same journal. The description of higher vegetation by HENNING E. PETERSEN gives enumerations in similar plot-groups (1 of 30, 2 of 64, and 2 of 121 plots) for 8 higher-plant dominants of the bog. In order of importance, they are *Calluna, Eriophorum vaginatum, Empetrum, Oxycoccus quadripetalus, Vaccinium uliginosum;* less frequently, *V. vitis-idaea, Rubus chamaemorus,* and *Andromeda*. — Each plot-group forms a square. Interval between plot-centers is one meter in each direction. The bryophyte plot-group with most species (14) was in Area C. From Olsen's table for it, a map was made of its 36 plots, showing species present in each. There are 4 species of *Sphagnum,* 7 other moss species, and 3 liverworts. *Hylocomium Schreberi* and *Hypnum cupressiforme* each occur in 25 plots, *Sphagnum rubellum* in 18, *Bazzania triloba* 14, *Aulacomnium palustre* 11, *Hylocomium splendens* 10, *S. magellanicum* 7. Spp. per plot, 3.44. — The map made possible a replicated count of species for aggregates of 2, 4, 6, 9, and 18

plots. Two independent methods of estimating equivalent one-piece areas for these aggregates gave fair agreement. The mean equivalent for 9 plots is 1.03 mlc.; for 36 plots it is 4.47 mlc. — It may be presumed that the plot-groups for the moss vegetation were located where higher plants were least prevalent. To the extent that they are present in the plots at Olsen's Area C, they may help to determine an Am-value larger than expected (5 mlc., or 20.23 sq. m.). This is larger than for any other of the European bogs of Table 22, but smaller than for any of the three moss-layer examples in Russian bogs (discussed in later section on mixed types of vegetation). Another likely reason for these large reference areas in moss vegetation is the considerable size frequently attained by many of the moss cushions or mats formed by plants of a single species.

LICHEN AND HERBACEOUS VEGETATION OF ROCKY SURFACES

In many mountain areas and in districts scoured by glaciers, a considerable proportion of the surface is rock, stony debris, or talus. Fragments may be of all sizes from large boulders to fine gravel. All degrees of stability likewise are found, from gravel slides and rock streams (as in the San Juan mountains of southwest Colorado) to firmly interlocked and compacted stony floors of angular fragments. Lichens are the usual plants of exposed dry surfaces. Mats formed principally of mosses are usual on shaded cliffs of humid canyons. Mixed-herb assemblages or inceptive grasslands develop in loose or compacted fragmented debris. While shrubs and trees may be early invaders, and may even assume dominance shortly after a surface is bared (as in some chaparral districts), their communities are not very different from other shrub and forest types.

TABLE 23. Lichen and Herbaceous Vegetation of Rocky Surfaces.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Parmelia omphalodes, Jungfrun	0.1355	0.548	11.3	16.3	3
Same, halophyte variant	0.1275	0.516	12.3	17.8	2
Lecanora deusta, Jungfrun	0.0235	0.0951	8.05	11.7	1
L. quartzina, upper variant	0.0738	0.299	6.31	9.12	3
L. quartzina, lower variant	0.105	0.425	3.66	5.30	3
Cladonia, shaded talus, n.e. Minn.	0.137	0.554	8.45	16.9	3
Arête de Sandgrat	4.27	17.3	15.4	22.6	2
Pierrier de Sandalp	18.5	45.7	27.0	39.2	2
Stipetum, sunny talus, Alps	22.4	90.8	21.3	31.4	2
Herbs, s. Alps border.	14.0	56.8	25.3	37.8	3

PARMELIA OMPHALODES ASSOCIATION, ISLAND JUNGFRUN. DU RIETZ (1921: 164, TABLE 21, FIG. 19). The coasts and islands of the Baltic afford much rock surface on which lichen covers are well developed. Du Rietz studied several lichen groupings, especially on Jungfrun. The brown foliose *Parmelia ompha-lodes* is clearly dominant in one of the more extensive types. In Du Rietz's plots

it covers half of the surface. The most frequent other species are *Cladonia squamosa* f. *muricella, Lecanora polytropa, C. Floerkeana* f. *carcata, C. coccifera* v. *stemmatina, Gyrophora polyphylla, P. fuliginosa, P. saxatilis*. The HAUPTVARIANTE has also 2 moss species in small numbers, and higher frequencies of *P. physodes*, and of a form of *C. gracilis;* while the HALOPHYTEN-VARIANTE has more of *Lecidea neglecta, P. conspersa, P. Mougeotii, Ramalina subfarinacea*, and *Rhizocarpon constrictum*. For the main variant, Du Rietz listed species in 10 16-sq.-m. quadrats, well dispersed in the lower part of the island, all on moderately exposed rocks. Each large quadrat was subdivided into 4- and 1-sq.-m. plots. The halophyte variant is at the upper edge of the *Sturmgürtel,* on rocks strongly exposed to wind and salt spray. There were many plots in this variant, located on different sides of the island. The 9 plot-sizes range from 1 sq. centimeter to 15 sq. meters. The large number of species recorded, 61 in all, is due to considerable variability of site, to scattering of the many plots, and to thoroughness of the survey of an inherently rich community. Dispersal and variability do not affect the species-area results, which are based only on average numbers of species per plot. Du Rietz summarizes these numbers on p. 207 in Table 32. Some of these are, for halophyte variant: 2.13 spp. in 4 sq. cm., 5.40 in 100 sq. cm., 9.22 in 400, 15.37 in 2500 (.25 sq. m.), 18.44 in 1 sq. m., 23.3 in 4, and 29.0 in 16 sq. m. A smooth S-curve based on these numbers fits the smaller areas well, the larger areas rather poorly (else a dependability rating "1" might have been justified). Du Rietz presents on p. 206 an interesting figure for this halophyte variant and 2 other lichen communities. Logarithm of average species-number per quadrat is plotted against logarithm of area. The decline in rate of species-increase as area is enlarged, is emphasized in his discussion. The preceding figure (p. 205) shows similar graphs for four communities (pine–dwarf-shrub, and heath). — Returning to the Hauptvariante in *Parmelia omphalodes* association, species numbers are: 17.58 in 1 sq. m., 22.29 in 4, 27.7 in 16 sq. m. The trend of its S-curve was judged largely from that of the halophyte variant.

LECANORA DEUSTA ASSOCIATION, JUNGFRUN. DU RIETZ (1921: 168, TABLE 23, FIGURE 19). This community is fairly extensive and characteristic on driest upper surfaces of rocks on the east coast of south Sweden and the many islands that fringe it. In its Jungfrun sites, the dominant lichen, a blackish crustose species, usually covers about 90% of the surface. Rarely does any of its companion species cover more than about 6%. The more frequent species are: *Lecidea furvella, Gyrophora polyphylla, Parmelia omphalodes* (dwarfed form), *Lecidea neglecta, Rhizocarpon geographicum, R. atrovirens, Lecanora polytropa, Cladonia coccifera* var. *stemmatina*, and *C. Floerkeana* var. *carcata*. The survey covers 10 16-sq.-m. plots (divided into meter squares), also 20 4-sq.-m. plots (divided into meter squares, and these into 0.25-sq.-m. and still smaller squares down to 1-sq.-cm.). In all, 48 spp. are recorded. — For 5 of the 9 plot-sizes, mean

nos. of spp. per plot run: in 1 sq. cm. 2.35 spp., in 25 sq. cm. 5.01, in 4 sq. dm. 9.73, in 1 sq. m. 15.6, and in 16 sq. m. 20.9 spp. The species-area curve fits the points fairly well, missing two of them by 0.7 species. It is a less steep curve than that for either variant of the *Parmelia* association, with more species at small areas, fewer at areas greater than 0.1 sq. m. In spite of the strong dominance of *L. deusta,* the smaller size of individual thalli in this more xeric site permits better representation of species in areas of a square foot or smaller. The less exposed site in which *P. omphalodes* dominates is perhaps the reason for its maximum floristic richness. Both the richness (with which steepness of the *Parmelia* curve is correlated), and the larger average size of plants, cause reference areas for both *P. omphalodes* variants to exceed those for *L. deusta* (Am-values are .548 and .516 sq. m. as contrasted with .0951 for L. deusta). One expects the lichen associations to have smaller minimum areas than any other types: the smallest heretofore has been .291 sq. m. for Du Rietz's near-arctic bog at Torneträsk. Of the 6 lichen communities treated, only *L. deusta* has a smaller Am value. A "complete stand" for L. deusta would cover 1.9 sq. m. or 0.47 milacre or 20.5 sq. ft., with 16 spp. The flat top of one large boulder could represent the association adequately.

LECANORA QUARTZINA ASSOCIATION OF THE STURMGÜRTEL, JUNGFRUN. DU RIETZ (1921: 171, TABLE 25, FIG. 19). This conspicuous yellow-green maritime rock-lichen dominates a narrow band just below the middle of the range of levels reached by waves during storms. Its maximum width is several meters; its lower part is differentiated somewhat from the upper. Du Rietz had difficulty finding large enough homogeneous areas in either variant. In the 15 1-sq.-m. quadrats of the lower-level variant, 9 species are recorded; in the same-sized upper-level aggregate are 16 spp. Three lower-variant species are not listed in upper-variant plots. The 7 plot-sizes range from 1 sq. cm. to 1 sq. m., but the 2 variants are not separated in the sizes below 1 sq. m. Curves for the variants were each based on only two points: one for mean no. of spp. per 1 sq. m. plot (6.07 for lower and 11.07 for upper), the other point for total no. of spp. (9 and 16) in one-piece area equivalent to each 15-plot aggregate. This was estimated at 18.07 mlc. Though dependability of the curves is low, results are in accord with expectations from comparison with the other lichen types. The Am values should be smaller than those for the *P. omphalodes* type because of the smaller plants in the Sturmgürtel. Am values should be larger than in the *L. deusta* type if, as is likely, the plants are on the average less minute.

CLADONIA COMMUNITY, SHADED BLOCK TALUS, NORTHEASTERN MINNESOTA. BRUCE FINK (1903). Fink studied lichens of cliffs along the north shore of Lake Superior. In 1897 he saw extensive talus areas of huge blocks of rock covered with larger Cladonias; "one such field covered more than an acre." In another talus about 1 mile w. of Grand Marais Bay, below the north-facing cliff called Howenstine Bluff, F recorded the species on 1 sq. rod of various-sized

blocks. The talus is 45 ft. high, with 35° slope. Trees of moderate size shaded all but its upper part. 21 species and varieties of *Cladonia* covered the plot. *C. gracilis* and its var. *dilatata* were especially abundant. *C. cristatella, C. verticillata* and a variety of it, *C. furcata paradoxa, C. fimbriata* and 3 varieties, and 5 other species were all "common enough." (Of the remaining 6 spp., *C. rangiferina, C. alpestris,* and *C. sylvatica* were the leading spp. in the other notable lichen types of the district.) — On the Howenstine talus were scattered logs on which smaller *Cladonias* were frequent. Fink thought it likely that the area had been burned (possibly 30 years earlier) and that the lichens had developed since. One of his photographs (Fig. 2) shows one square foot "with a dense growth of *C. gracilis* and 8 or 9 other *Cladonias* in small numbers." — If we consider that 19 kinds of *Cladonia* on 1 square rod and 8 kinds on 1 square foot are somewhat more representative of the general condition of this lichen cover, the 2 points so determined are available for a tentative species-area curve. A square rod (16.5 feet square) is 6.25 milacres; 1 sq. ft. is .02295 mlc. A likely position for the curve puts the flex point at about .025 mlc. The Am value from the curve, 0.137 mlc. or .554 sq. m., is slightly larger than that of Du Rietz's *Parmelia omphalodes* association (Hauptvariante).

ARÊTE ROCHEUSE DE SANDGRAT, "HAUTES ALPES," ELEV. 2780 M. JACCARD (1914: 16, TABLE 2). Jaccard described this as an example of an extreme site excluding all but a few species, making it possible for two plots to have identical species lists. The area examined had 24 species; 21 of them occur in one group of 12 contiguous 1-sq.-m. plots; plots 4 and 5 have the same 11 spp.; plots 6 and 7 have the same 10 spp. Species occurring on all 12 plots are *Alsine Cherleri, Chrysanthemum alpinum, Cetraria islandica, Gentiana bavarica,* and *Luzula spicata. Silene exscapa* is in 11 plots, *Saxifraga bryoides* in 10, *S. exarata* in 9, *Potentilla frigida* in 8. — In 1-sq.-m. plots, av. no. of spp. is 11.0; combinations of neighboring plots gave 13.36 spp. in 2 sq. m., 15 in 3, 16 in 4, and 18 in 6. The 7 available points determine the lower section of an S-curve. Its slope is moderate because rate of increase is low, and because, with plants small and not crowded, number of species per plot is relatively high at small areas. Reference areas are small as compared with floristically rich rocky areas, such as Jaccard's plot-group III in the Pierrier de Sandalp, and his *éboulis morainique* in the same district.

PIERRIER DE SANDALP, LINTH VALLEY, ALPES GLARONAISES, ELEV. 1938 M. JACCARD (1914:6-9, TABLE 1). The site is a fairly old alluvion or terrace of large pebbles, on one side of the Linth River, 1 to 2 meters above the torrent. It is over 200 m. long and about 30 m. wide. Its cover is a mixture of many herbs, mostly perennial, including 8 grass species. A moss and 3 *Salix* species are also among the 70 species recorded in the whole area examined. Detailed listings were made for four groups of 1-sq.-m. plots; the groups are separated by gaps of 5, 20, and 50 m. Groups I, II, and III are much alike; IV has a sparser cover

and is on a deposit not so old as the main part. (It was not included with the others in the species-area treatment.) The apparently stable cover is principally of the characteristic and generally-distributed perennials *Anthyllis vulneraria, Epilobium Fleischeri, Gypsophila repens,* and *Linaria alpina.* Others include *Euphrasia salisburgensis, Kernera saxatilis, Festuca pumila, Oxytropis* (2 species), *Poa alpina, P. minor, Saxifraga aizoides.* Most of these are on fewer plots in plot-group IV. — For the 4 sets of plots, pertinent figures are summarized thus:

Group	Area, sq. m	Spp. per plot	Total spp.
I	19	4.37	19
II	21	7.05	32
III	18	9.61	36
Mean	19.33	6.97	29
IV	27	2.81	19

In addition, there is a total of 45 species in the 58 sq. m. of the aggregate of the 3 plot-groups. The estimated one-piece equivalent of the aggregate is 43.1 mlc. — The Am-value, 18.5 mlc., is in the range of sizes found for more open grass lands. In this case, it is likely that competition among plants of the pebbly terrace does not exclude immigration of almost any species from surrounding communities. Jaccard pointed out that the species present are a chance selection from the available flora, and that they show no particular adaptation to the site. These circumstances are in accord with a species-area curve which is only moderately convex in its upper part: the rate of species-increment persists well into rather large areas.

A tentative curve drawn for plot-group IV, though based on insufficient data, suggests an Am of 24 mlc. (59.4 sq. m.), Sm of 25.4. This result is expectable, because of the sparser plant cover and scantier flora as compared with groups I to III.

Jaccard briefly describes also the debris-slope (30 to 35°) which he calls the PIERRIER D' ÉBOULIS MORAINIQUE, less than 1 km. from the Linth River terrace. The list of species is much the same. He studied a homogeneous area of 40 sq. m. in which species-numbers per sq. m. were 8 to 13, and in which the first 13 plots showed 28 spp. A tentative curve for the éboulis gave a likely Am of 18.1 mlc. (44.8 sq. m.), with 40.6 species.

STIPA CALAMAGROSTIS ASSOCIATION OF SUNNY TALUS SLOPES, GLARNER ALPS. HANS JENNY (1930: 164-178, TABLE 1, FIG. 8). This community is found on south and southeast slopes in calcareous districts at moderate elevations (Montane Zone). It is a heterogeneous assemblage of species; rock-plants, ruderals, plants of forest and shrubby borders, of sparse and stony grasslands. The characteristic species are *Stipa, Vincetoxicum officinale, Galeopsis angustifolia, Reseda luteola, Epilobium rosmarinifolium,* and *Calamintha nepetoides.* Many of the other species occur also in the rocky or stony grasslands of the southern

base of the Alps (as in the next example from Jäggli and Jaccard). — Jenny gives a detailed association table, from which 7 Aufnahmen for stated areas were used to make a composite species-area curve for the type. One other area, No. 4, approaching optimal phase of development, is much richer in species composition than the 7 chosen; 3 areas, Nos. 6, 7, and 10 are obviously poorer in species. It was found that the different Aufnahmen could not be divided into two or three groups which agree within themselves as to texture of rock fragments, stage of development, elevation, location, and degree of instability of surface materials. (Elevations range from 480 to 900 meters; most of the slopes still move somewhat; steepness is 30 to 36°; extent of the Aufnahmen varies from 16 to 100 sq. m.) — Species-numbers at small areas were found by subdividing Jenny's map of a 15-sq.-m. plot. This is his Fig. 8, p. 176, showing the condition in 1926; the plot is on a slope laid bare in 1919 by a rock-slide. The map shows individuals of 19 species. Some of the species numbers used for plotting are:

Milacres	0.232	0.926	3.95	12.35	24.71
Species	4.56	11.25	21	26	32

The Am value found is large: since usually less than one-fourth the surface is covered by plants, the same number of species might be found in one-fourth as much area if occupation were nearly complete. It may be presumed that reference areas will be progressively reduced as (or if) the vegetation is able to develop into a continuous cover of some type other than the Stipetum.

Some of the other rock communities in Jenny's article are equally worthy of species-area study. His bibliography includes citations of many other fine studies of the vegetation of cliffs and debris slopes.

HERBACEOUS VEGETATION OF ROCKY AND THIN-SOILED SUNNY SLOPES, TICINO AND LOMBARDY. M. JÄGGLI (1928), AND P. JACCARD (1914). Jäggli describes Monte di Caslano, a bold rocky hill nearly surrounded by a western arm of Lake Lugano. On the steep slopes to the lake on south and southeast sides, with dolomite substratum, the nearly bare surface is strongly insolated. On a plot of 4 sq. m. in the *vegetazione rupestre,* Jäggli listed 5 moss species and 16 flowering-plant species. All the mosses and 8 other species are marked as characteristic of rocky sites. These 8 are *Sesleria coerulea, Carex humilis, Dianthus Caryophyllus, Fumana ericoides, Thymus Serpyllum, Teucrium chamaedrys, Globularia cordifolia,* and *Leontodon tenuiflorus.* A supplementary list for similar sites nearby names 7 more species. — A grassland, sparse and xeric, covers about a third of the dry south and southeast sides in small areas among rocks and among shrubs and stunted oaks. In some places this *praterie magre asciutte* appears to be stable. Especially where it is well enough developed to make the cutting of wild hay feasible, this practice tends to prevent replacement by the *boscaglie xerofili.* Jäggli's example of this praterie, recorded in August, 1927, covers 50 sq. m. on a 28° slope facing southeast. Soil is coarse and shallow (10-15 cm.). The plants are mostly herbs, with a few suffrutices and suffrutescent herbs. Of

the 37 species scattered sparsely over the area, 5 grasses, a sedge, and a lily are fairly numerous. They are *Bromus erectus, Andropogon Gryllus, Carex humilis, Molinia coerulea, Sesleria coerulea, Anthericum ramosum,* and *Brachypodium pinnatum.* This list of 37 species includes 9 of the 16 species of the 4-sq.-m. rock plot, suggesting close kinship of rock vegetation to praterie. A supplementary praterie list gives 27 other species in similar sites on the same part of Mt. Caslano. — Jäggli relates this inceptive grassland of rocks and thin-soil slopes to the Xero-Brometum erecti described by J. Braun in the southern Cevennes, and names species common to both.

A grassland described by JACCARD (1914: 19) as a very dry and meager prairie is situated ABOVE MENAGGIO on Lake Como (only about 17 miles e.n.e. of Mt. Caslano). The soil is shallow. A few moss species and *Festuca ovina capillata* form the chief cover. *Bromus erectus, Sesleria, Danthonia procumbens, Carex Baldensis,* and many herb and some few low-bush species are scattered sparsely through the area. Jaccard lists 32 species on a 25-sq.-m. plot. Some few of these are the same as at Mt. Caslano: in more cases the same genera are common to both localities. It seems that the 3 plots are nearly enough of the same type to be used together for a species-area curve. The Am-value found, 14 mlc., is fairly large. This is an expectable consequence of the incompleteness of the plant cover and the rich supply of species in surrounding areas. Jaccard says the prairie above Menaggio is a peculiar association of species which, generally, occupy habitats that are very different.

ALVAR VEGETATION, AND OTHER HORIZONTAL ROCK-BARRENS. It is regretted that examples of these types are not included among those here studied. Alvar is the name for bare or very thinly-covered outcrops of calcareous rock, best developed in islands of the Baltic Sea, especially Öland. The first plants are lichens, with various crevice-plants in the joints. These rock-pavements and the concomitant development of soil and of vegetation over them have been well described by C. FERDINANDSEN (1916), by Du Rietz, and others.

STRATIFIED COMMUNITIES; MIXED VEGETATION AND COMPLEXES COMPRISING UNLIKE GROWTH-FORMS

It is not profitable to attempt a sharp distinction between stratified compound vegetation in which at least the top stratum is apparently homogenous, and mixtures or complexes in which horizontal discontinuity is obvious. A conspicuous example of such a mixture is that of the Boulder mesa-top, next described. Three forests with their strata illustrate some of the complexities of the familiar type. The moss, dwarf-shrub and (usually scattered) pine components of raised bogs in Russia, followed by relatively simple two-phase mixtures of bushes or shrubs with grass or herbs, conclude the series of vegetation-units treated in this article.

TABLE 24. Vegetation Complexes of Unlike Growth-Forms.

Complexes and their components	Am, mlc.		Am, sq. m.		Sr	Sm	D
Mesa-top near Boulder:							
All species		24.9		101	26.25	37.7	1
Woody species		198		802	9.89	15.0	1
Herb species		10.6		42.9	16.2	24.2	1
Mixed decid. forest, Indiana:							
All species		226		913	59.4	89.4	2
Trees alone, 3″ +	1	665	67	380	14.25	20.7	3
Shrub species		195		790	8.73	13.05	2
Herb species, including ferns		199		805	33.8	50.9	2
Conifers + decid., Maine:							
Trees, 3-inch diam. +		519	2	100	8.00	12.05	3
Trees, 1-inch diam. +		225		910	9.45	14.2	3
Shrubs		142.5		577	7.68	11.5	3
Herbs		12.1		49.0	15.0	22.3	3
White pine forest, Wis.:							
Trees, 3-inch diam. +		860	3	480	5.79	8.44	1
Herbs + small woody plants		6.09		24.6	24.6	37.8	3
Herb species		5.85		23.7	16.7	25.0	3
Raised bogs, central Russia:							
Rubskoje Moor, field layer		21.6		87.5	8.57	12.7	2
moss layer		6.35		25.7	2.36	3.44	2
Krupino Moor, field layer		7.11		28.8	6.14	8.93	3
moss layer		12.6		51.0	3.00	4.52	2
Mironowo Moor, moss layer		10.5		42.5	3.81	5.70	3
Sagebrush—grass, N. D.:							
Grassland with A. cana		10.8		43.7	33.8	49.2	3
Grassland without A. cana		8.48		34.3	33.6	48.9	3
Short-grass—bush, Colorado:							
Grassland with bush		7.14		28.9	22.7	34.0	2
Bush phase		2.77		11.2	2.59	3.94	2
Grass phase		8.13		32.9	20.3	29.9	2
Bush—short-grass, S. L. V.:							
Bush with grassland		101		408	22.65	33.05	3
Chrysothamnus—Gutierrezia		27.0		109	3.93	5.73	3+
Short-grass phase		125.5		506	18.7	27.2	3
Bush—grass garigue, France:							
All species		5.135		20.77	26.4	38.8	3
Bush phase		6.65		26.9	10.8	15.8	3
Grass and herb phase		4.315		17.45	15.6	23.1	3
Creosote-bush with herbs:							
Woody spp.: C. V.	1	908	7	721	3.63	5.32	3
G. V.		530	2	145	1.58	2.29	3
Herb spp.: Coachella Valley		1.93		7.81	18.0	25.7	3
Gila Valley		2.45		9.91	16.7	24.0	3

MIXED VEGETATION OF MESA-TOP NEAR BOULDER, COLORADO. VESTAL, SEPTEMBER, 1944. This complex can be described as rock lichens + inceptive grassland + mountain bunch-grass + dwarf-shrub + shrub + foothill conifers (here mostly stunted). Descriptions of these components are included in three papers (Vestal 1914, 1917, 1919). The place studied is near the northwest edge of Horse Mesa, one of the several high "mesas" south of Boulder. (These are

sloping high terraces with thick cap of rocky alluvium). The location is above and a few hundred feet south of Bluebell Spring (which is in Bluebell Canyon). These mesas and their partial cover of rock pines (*P. ponderosa* var. *scopulorum*) were the subject of early papers by RAMALEY, DODDS, AND ROBBINS (UNIV. COLO. STUDIES, VOL. 6, 1908). One part of the very rocky mixed area here treated was mapped in 1919 and at two later times. It is a grid of 42 10-foot squares, and includes a few old but not large pines and numerous small pines dating from about 1883. For more intensive study of the herb and dwarf-shrub vegetation in 1944, a grid of 52 5-foot squares north of the mapped area was used. It included 3 pines 1.5, 2, and 4 feet high, with a few seedlings and 5 stumps (the largest 6.5 inches in diam.), and 1 small tree (6.5 feet) and 1 3-inch seedling of *Pseudotsuga taxifolia. Juniperus sibirica* was represented by mats or seedlings in 15 of the 52 squares: *Arctostaphylos uva-ursi* in 19 squares; the spiny dwarf-shrub *Ceanothus Fendleri* in 7; small individuals of *Rhus glabra, Prunus melanocarpa, P. pennsylvanica,* and *Rubus deliciosus,* in 5, 2, 1, and 1 of the 52 squares. Most of the herbs had higher frequencies. Worthy of mention are *Andropogon scoparius, Muhlenbergia gracilis,* a *Carex, Koeleria, Danthonia; Artemisia, Chrysopsis, Aster, Penstemon, Comandra, Sedum.* The lichens on surface rocks and boulders were omitted from the count, but mosses (a *Polytrichum* or closely-related moss, and a *Grimmia*), were included. They were usually on the soil itself, either at the north base of rocks or in places subject to erosion (they tend to retard surface washing). In one square *Polytrichum* covered 160 sq. inches.

From the detailed table made in the field, various combinations of plots were made, giving species-numbers for 14 plot-sizes (1 to 52 squares). To give data for larger sizes, treeless parts of the older grid, and another treeless and very rocky area south of the older grid were searched for additional species. Area 1 + Area 2 make 196 squares; 1 + 2 + 3 make 340 squares. Translated to milacres, part of the array of areas and species-numbers (with mosses included in "all species") appears as follows:

Milacres	0.57	1.15	2.30	4.59	7.46	14.9	29.8	112.5	195.1
Woody spp.	1.25	2.10	3.15	4.25	5.25	7	9	13	16
Herb spp.	9.35	13.04	16.45	20.4	22.4	25	26	37	41
All spp.	10.75	15.44	20.22	25.7	29.1	34	37	52	59

From these figures, S-curves were made for woody species alone, herb species alone, and for all species. The resulting Am, Sr, and Sm values appear in Table 24. For either woody species or grassland, the reference areas are several times as large as they would be if other growth-forms were not present. In places, especially near the edge of the mesa-top, sizable boulders cover almost half the surface. Whatever space is occupied by actual trees or tree-clumps is likewise unavailable to shrubby cover or to grassland.

The components of this mosaic are prominent among those encountered over the gravelly or rocky surface of the granite foothills and lower mountains of

the Colorado Front Range and other parts of the Southern Rocky Mountains. The complex is thus fairly typical of the lower yellow-pine zone in those areas that are neither grassland nor actual forest. Aggregate area of this mosaic probably exceeds 2000 sq. miles. Similar mixtures with some of the same components cover much wider areas in the mountains of the west.

MIXED DECIDUOUS FOREST: TREES, SHRUBS, HERBS. NASH'S WOODS, POSEY COUNTY, S. W. INDIANA. S. A. CAIN (1934). The location is 5 miles s. e. of New Harmony. In a 45-acre stand, 25 acres of old-growth forest are dominated by *Liriodendron, Quercus alba, Acer saccharum*, and *Nyssa sylvatica. Fraxinus lanceolata, Ulmus fulva, Sassafras, Cornus florida*, and *Cercis* are numerous. Shrubs and vines are well represented; 7 ferns and many herb species form the ground cover. In each of 25 places, Cain established plots of 6 sizes: 1, 2, 4, 25, 50, and 100 sq. m. These were later supplemented by 9 and 16 sq. m. From Cain's frequence table on pp. 542-44, separate data were taken for trees, shrubs, herbs including ferns, and totals for all species. Mean number of species per plot for each group was found from frequencies (by finding the total number of "occurrences" and dividing by number of plots, 25). For areas larger than 100 sq. m., the number of shrub or of herb species in an aggregate of 25 plots was the basis for an estimate of the somewhat smaller number of species in a single compact area of the same extent as the aggregate. Also, the larger one-piece area having the same number of species as an aggregate, could be estimated (I-conversion).

Since the frequencies for tree species included small sizes, conversion was essayed to give data for trees of 3-inch diameter and larger. For such trees, the density was assumed to be 136 per acre. A table was prepared showing number of plots of three sizes in which each tree species occurred (the sizes: 1, 25, and 100 sq. m.). A column was added for likely number of individuals to give the stated number of occurrences. Thus for 28 tree species represented in 25 100-sq.-m. plots by 377 occurrences, a likely number of individual trees of all sizes was estimated to be 1054. For trees 3″ or larger on the same plots, the likely number is 84 (from density of 136 per acre on .6178 acre). Likely numbers for trees of particular leading species were suggested from data given on Cain's p. 556; for the other species from the table of occurrences. A second table of occurrences was prepared for the 84 trees 3″ and larger. About 18 species are represented by these 84 individuals. Av. no. of spp. per plot (again from no. of occurrences), comes to 0.8 in 25 sq. m., 2.96 in 100 sq. m. In the aggregate of 25 1-sq.-m. plots there are 2 spp.; in the 25-sq.-m. plots, 12 spp.; in the 100-sq.-m. plots, the 18 spp. mentioned. From species-numbers thus roughly approximated, an S-curve was made. It gave the Am value of 1665 milacres. (This compares with 1428 to 2761 for other old-growth mixed forests in Indiana: see Table 2 in this article.)

For the shrub and vine species, the herb species, and the complete list of

species, it was relatively simple to find species-numbers for the various plot-sizes, and to make a species-area curve for each group of species. The curve for shrubs and vines is not the same as a curve for all plants of the shrub stratum, since many young trees are part of that stratum. Similarly the herb group does not include the tree seedlings and low shrubs which form part of the field layer. Probably the rather large reference-areas for the herb group is partly due to this intermixture of woody plants, as well as to complete occupation of part of the ground-space by solid thickets of shrubs or young trees. The minimum area for herbs is 199 milacres, as compared with an ordinary range of 48 to 81 for herb ground-cover under forest (see Table 19). This Am value for herbs of Nash's Woods is larger than that for the shrub group, which is 195 milacres, a result that could hardly be foreseen. (This difference cannot be depended upon, as the error of determining Am for either group of species is probably any amount up to about 20 milacres.) The shrub Am value, 195 milacres, compares with an ordinary range of 46 to 96 milacres, with larger extreme values 198 to 450 (see Tables 11, 8, 20).

One may ask whether a composite curve for plants of such greatly differing size and character as mature trees, tree seedlings, shrubs, tall and low herbs, with areas computed from the curve, can have any real meaning. The author does not see any significance therein; his objective was to find how a composite curve compares with curves for constituent parts of the forest. In making the composite curve, one had to decide whether to use data for all trees or only for the large trees. It is obvious that for a forest which includes many seedling and small trees, omission of an important part of the lower strata would seriously distort representation of the forest as a whole. Therefore the original given data for trees were used. As might be expected, reference areas for all plants in combination prove to be somewhat larger than for either shrubs or herbs, but much smaller than those for the sizable trees.

MIXED CONIFER–HARDWOOD FOREST (FIR–RED MAPLE–SPRUCE), N. OXFORD COUNTY, W. MAINE. H. J. OOSTING AND J. F. REED (1944). The type locally designated spruce flat, occupies well-drained, moist soils near streams. The stand studied is at lat. 44° 38′, near Andover, and adjacent to Horseshoe Brook. It has been cut several times, last in 1924; age of larger trees averages 57 years. Dominant trees are *Abies balsamea, Acer rubrum, Picea rubens,* and *A. saccharum. Tsuga canadensis* and *Pinus strobus* are sparingly present. *Acer spicatum, Betula lutea,* and *Fraxinus americana* are abundant in the second story; the ash is growing into the top stratum. Tall shrubs, especially *Corylus rostrata, Alnus incana,* and *Hamamelis virginiana,* occur with the sub-dominant or second-story trees. Other shrubs include species of *Cornus, Viburnum, Rubus, Ilex,* and *Lonicera.* Characteristic herbs are *Trientalis, Oakesia sessilifolia, Cornus canadensis, Maianthemum, Lycopodium* species, and *Clintonia.* — The stand was sampled in 10 places, each with 3 plot-sizes: 100, 16, and 1 sq. m.

Trees 1″ + (one inch diam. and larger) were recorded separately for top story and second story. In all, 673 trees comprised 16 spp., with 7.4 spp. per 100-sq.-m. plot. Young trees 1 to 10 ft. tall, tree seedlings under 1 foot, and shrubs (10 spp.) were recorded from 10 16-sq.-m. plots; herbs (18 spp.) from 10 1-sq.-m. plots. Relatively simple adjustments of data were required for trees 1″ +, and for shrub and herb components, to make species-area curves possible. For trees 3″ +, relative densities were employed. Density of top-story dominants (given on p. 195) comes to 238, and of subdominants (p. 196) to 435, in 1000 sq. m. This makes 673 trees in 247.1 mlc. or 2746 trees 1″ + per acre. If it is assumed that somewhat less than half the dominants have reached or exceeded 3″ diam. (few can have grown much larger), a tentative ratio of trees 3″ + to trees 1″ + is 108 to 673, or 0.1604. From this, the density of 3″ + trees should be 482 per acre. One can now tabulate tree-numbers of the two diameter-limits for different plot sizes (7 were used), and one can also put down for trees 1″ + the number of species at each plot-size, as read from the species-area curve for those trees. Then by C-conversion (use of species-individuals curves) one finds approximate no. of species for the no. of trees 3″ + at each plot-size. This gives data for a species-area curve for trees 3″ +. Reliability of reference areas from such a curve is low, but a rough comparison with the tree-layer of other forests is thus made possible.

Some of the species-numbers for groups of species and for layers are shown in the accompanying table. 38.97 mlc. is the compact area equal to the aggregate of 10 16-sq.-m. plots; 71 mlc. is the est. 1-piece equivalent of the same aggregate (equiv. in having the same no. of spp.); 450 mlc. is the est. 1-piece equiv. of 10 separated 100-sq.-m. plots. Note that line c, for trees 1″ +, may also serve for the tree-crown layer (perhaps the figures should be slightly enlarged to include tallest shrubs accompanying second-story trees). Note also that line g, for trees of all sizes, is not the sum of c, e, and f.

TABLE 24a. Approximate Species-Numbers at Certain Areas, Spruce Flat.

Area in milacres	0.247	3.897	38.97	71	450
a. Herbs	6.0	17.3	26.7	28.5	33.0?
b. Shrubs	1.7	2.8	8.5	10.0	13.6
c. Trees, 1″ +	0.4?	2.3	9.0	10.9	16.0
d. Trees, 3″ +	0.1?	1.3	5.2	6.9	11.8
e. Tree seedlings, < 1 ft.	2.5?	4.9	8.5	9.0	17.5?
f. Young trees, 1-10 ft.	1.1?	3.7	6.0	7.0	17.0?
g. Trees, all sizes	2.6?	5.2?	9.5˙	11.0	19.0?
h. All species (a + b + g)	10.3?	25.3?	44.7?	49.5?	65.6?
i. Herb layer (a + e)	8.5?	22.2	35.2	37.5	50.5?
j. Shrub layer (b + f)	2.8?	6.5	14.5	17.0	30.6?

The table shows how much the tree seedlings and young trees contribute to herb and shrub layers. The question is raised: Which is the real synusia or component of a several-layered stand, the group of species of one growth-form, or

the layer? A group of similar species, such as coniferous trees, usually takes up space in more than one layer; a layer (except the topmost) comprises one or more components which attain maturity in that stratum, plus young plants which will later belong in a higher stratum. Or does each group of species form different synusiae in different layers? No answer will be attempted to these questions. Students of vegetation have become increasingly aware of the very great complexity of a mixed forest; the situation just posed is merely another example of that fact.

In considering the minimum areas found for different elements of the mixed spruce stand as shown in Table 24, one notes that the Am value for trees 3″ + (519 mlc.) is smaller than that of any high-density deciduous stands of Tables 2 and 3, such as Potzger's No. 39 (868 mlc.) and McCoy's stands I and V (718 and 799). In general, stands of conifers or of conifers with slow-growing hardwoods have higher densities and smaller reference areas than deciduous stands. This same Am of the spruce flat likewise is smaller than that of Potzger's northern pine forests (678 and 860 mlc.) This is likewise expectable in a cut-over stand of young trees as compared with old-growth stands. — The minimum areas for shrubs in the spruce flat (142.5 mlc.) and in Nash's Woods, Indiana (195 mlc.) are larger than in a majority of bush and shrub types of treeless areas. — The very small Am value for herb cover in the spruce flat (12.1 mlc.) as compared with ordinary range of 48 to 81, from Table 19, suggests that the 1-sq.-m. plots may represent local patches of pure herb cover rather than average condition of the forest floor.

WHITE PINE FOREST, VILAS CO., N. WISCONSIN. J. E. POTZGER (1946: 225). The trees of this notable stand, mostly *Pinus strobus,* on the property of the Dairymen's Country Club, between Big Crooked and Wolf Lakes, have already been included in the section on forests of middle latitudes. Potzger's Table 23 gives details of density and frequency for plants of the ground cover, in 20 1-sq.-m. plots. There are 26 herb species, of which *Maianthemum, Waldsteinia, Trientalis,* and *Pteridium* are most abundant and frequent. Tree seedlings of 8 species occur. Only *Acer rubrum* and *A. saccharum* are important. A relatively small number of young or small shrubs in 5 species brings the list for the 20 plots to 39 species. — The average number of species per plot is for herbs 6.65, for tree seedlings 2.25, for shrubs 0.5, for all three groups 8.95. The one-piece area estimated to be equivalent to the 20 plots is 7.17 milacres. Two species-area curves were made, one for the low-plant layer as a whole (the 3 groups of species), the other for herb species.

Comparison of ground cover in this forest with that of either Nash's Woods (deciduous) or the conifer-deciduous mixture in Maine seems not to be feasible. Such comparisons probably must await new field studies especially designed for the purpose.

THREE-LAYERED RAISED BOGS, CENTRAL RUSSIA. N. J. AND S. KATZ (1926:

190-191). The authors investigated Minimiareal after the methods of Du Rietz "auf den Hochmooren Mittelrusslands weit verbreiteten Assoziationen der Torfmoosreichen Zwergstrauch und Gras-Nadelwälder *Pinus silvestris–Cassandra calyculata–Sphagnum recurvum* und *Pinus silvestris–Eriophorum vaginatum–Sphagnum recurvum.* . . ." The two associations were each studied in 3 localities: Rubskoje Moor (farthest east) in Govt. Iwanowo-Wosnesensk, Distr. Tejkowo; Krupino Moor, 336 km. w. s. w. of Rubskoje, in Govt. Moscow, Distr. Wolokolamsk; and moors between Mironowo and Saprudje in Govt. Moscow, Distr. Leninsk. This location is 150 km. from Krupino, and 200 km. from Rubskoje. Separated quadrats of three sizes, 1, 4, and 16 sq. m., are summarized in the authors' tables. Pines of tree size are listed in from 71 to 91% of the 1-sq.-m. plots in all six sets of data. In both associations the dwarf shrubs are *Vaccinium* spp. (*V. oxycoccus* most frequent), *Cassandra, Ledum,* and *Andromeda.* (Most botanists use for *Cassandra* the genus name *Chamaedaphne.*) Small pines are frequent in one, and present in 3 other sets of plots. The grass-like plants are *Eriophorum, Carex pauciflora, C. dioica, Scheuchzeria,* and *Molinia.* Dicot herbs are *Drosera* and *Melampyrum.* — The ground layer is dominated by *S. recurvum* and *S. medium,* with 6 other moss spp. and (in 2 sets of plots) *Cladonia rangiferina.* — Species-area curves for field layer and moss layer were made for the two sets of data having most species: at Rubskoje the *Cassandra* Association (RC), and at Krupino the *Eriophorum* Association (KE). The moss-layers for both associations at the location near Mironowo (MC and ME) were also studied. The one-piece area estimated to be equivalent to an aggregate of plots (designated I) varies with size and number of plots; where the same number of species accompanies more than one size of equivalent area a compromise value for the area was adopted. Species-numbers used as the basis for five curves are tabulated herewith, as well as species-numbers for moss layer in the other three stands.

Stand	Layer	.247 mlc.	.494 mlc.	3 954 mlc.	I, spp.	I, size in mlc.
RC	Field	5.64	6.63	8.4	17	199
RC	Moss	1.79	2.25	3.0	5	199
KE	Field	4.56	5.95	7.6	13	128
KE	Moss	1.95	2.40	3.4	6	128
MC	Moss	3.22	3.47	4.4	8	213
ME	Moss	2.407	2.582	3.5	5	87
RE	Moss	1.98	2.025	2.1	3	199
KC	Moss	2.281	2.312	2.5	3	88

Results from the curves are unexpected in two ways: for one stand, KE, the reference areas for field layer are considerably smaller than for moss layer (Am values 7.11 and 12.6 mlc.). Location and form of the field-layer S-curve for KE are uncertain, whereas for RC, a regular S-curve exactly fits the four given points. Also, for all five curves, reference areas are much larger than might be expected from earlier determinations of Minimiareal for this and similar types of vegetation in northern Europe. Katz and Katz followed Du Rietz in

using only the field layer for determining Minimiareal; they found no increase in number of constant species from the 4-sq.-m. plot-size to the 16-sq.-m. size, and rightly concluded that the Minimiareal (an area based on adequate content of first-order constants) lies between 1 and 4 sq. m. If any of the reference areas used in the present study might correspond to Minimiareal it is the "smallest representative area," Ar. Yet the lowest Ar value for any of the five raised-bog curves is 5.14 sq. m. (for moss layer in RC). The lowest field-layer Ar (5.75 sq. m. in KE) is perhaps erroneous. The only dependable comparison with the Minimiareal of less than 4 sq. m. is the field-layer Ar for RC, which is 17.5 sq. m. If a smallest representative area based on all species is thus 4 to 7 times as large as that based on first-order constants (those few species which are most numerous and most generally distributed), the contrast between these few and the other species is seen to be highly significant. From at least the statistical viewpoint, Du Rietz's emphasis upon the constant species is amply justified. — Another illustration of the contrast between the generally distributed species and the others (which seems to call for some consideration of the other species also) is the fact that although no new constants are added between 4 and 16 sq. m., yet the increment in total species-number is almost invariably greater between those two areas than in the other four-fold increase from 1 to 4 sq. m. This is true in all ten lines of the foregoing tabulation of species-numbers in the high moors, as applying to absolute value of the species-number increment. Thus in RC field layer, the increment in mean species-number per plot is 0.99 from 1 to 4 sq. m., 1.77 from 4 to 16 sq. m. *Ratios* of increase are likewise greater from 4 to 16 than from 1 to 4, except for the already suspect field layer of KE. For field layer of RC the ratio of increase from 1 to 4 sq. m. is 1.175, from 4 to 16 sq. m. it is 1.267.

When the species-numbers at particular areas are plotted on semi-log paper, the result of the foregoing relations is that the section of the species-area curve which lies between 1 and 16 sq. m. is conspicuously concave, which means, if species-increase continues at accordant rate, that even the smallest reference area, Ar, might be expected to exceed 16 sq. m. Yet for some sets of data in which species-numbers are small, it is questionable whether any section of the curve will yield a two-fold increase in species-number with a fifty-fold increase of area. The further fact that at 1 sq. m. the curve is nearly level makes one suspect that if it were extended into smaller areas, a second steeper section would be found. Unfortunately, data for a range of small areas are not available. In some other bog and dwarf-shrub communities and in chaparral there have been earlier suggestions that their species-area curves are double curves: that the few first-order constants have attained a nearly level upper section at one or a few square meters, at which size other species are at the bottom of their curve. Field investigation into this possibility should embrace a series of replicated one-piece areas, in steps representing about a four-fold increase in extent, and ranging (in bogs) from $\frac{1}{256}$ or $\frac{1}{64}$ sq. m. to perhaps 1024 sq. m. The preparation of

curves from so dependable a series of areas in fine-textured communities of few species should decide incidentally whether in some communities no part of the curve will yield twice as many species with fifty times the extent, and if so suggest criteria for sufficiency of area in such communities.

ARTEMISIA CANA BUSH, WITH BOUTELOUA–AGROPYRON–STIPA. WESTERN NORTH DAKOTA. HANSON AND WHITMAN (1938: 61, 75). The authors' Test Area 18, representing their Type 5, is one of three examples in which *A. cana* is the dominant bush. Area 18 is well grassed. The site is a low terrace above Garner Creek on Olstad Ranch, 16 miles s. e. of Sentinel Butte. Soil is brown clay, without excess of solutes, and with subsoil moisture available at all times. *A. cana* is in certain respects, such as stature, habit, and spacing, similar to *A. tridentata* of farther west. *B. gracilis, A. Smithii,* and *S. viridula* are the only notable species of the grassland phase. (*S. viridula* is common at borders of thickets at the front of the Rocky Mountains; it is significant in only this one of Hanson and Whitman's 10 types).

From statement of size of bushes, and from data in Hanson and Whitman's Table 1 on relative importance of species, supplemented by random spotting of bushes on a hypothetical map including 15 plots, the following approximate figures were inferred. The average bush covers 10 sq. ft. within an area of 36.7 sq. ft. Bushes per acre, 1187. Percentage of area occupied by bushes, 27.3. Presumed frequency of bushes, 60% (in 18 of 30 separated 1-sq.-m. plots). Stated av. no. of spp. per plot 12.9; 40 spp. in the 30 plots. One-piece equivalent area (to include the 40 spp.), 11.76 mlc. From these figures it was possible to construct a curve for this two-phase mixture, with results as in Table 24 (minimum area 10.8 mlc.).

THE BUSH PHASE. It is impossible to apply to a one-species community or vegetation-component the same criterion for sufficiency of area that is used for a unit with numerous species. An approach can perhaps be made by considering a characteristic that is usually definable: spacing. If spacing is nearly uniform, as it frequently is in xeric bush or shrub, or in many stands of juniper or of pinyon in western North America, one can determine the area required to include a certain minimum number of individual plants of the species. It will be necessary for many students of vegetation to reach agreement on the value of this minimum number. Theoretically, the smallest area which will almost surely contain one individual of representative size or age, is big enough, if one knows that other sample areas of the same size will contain the same species and no others. The smaller the arbitrarily-adopted minimum number, the greater will be the variability as among sample-plots in one stand, or as between different stands. To reduce variability, particularly if one is studying stands that are far from uniform in spacing, a number no smaller than 10 is suggested for field trials. In the other direction, it has been found that the number of individuals in Am or minimum area for a mixed community with many species ranges from

504 down to 100 or fewer. The figure 504 was found for trees 3″ + in 4 acres of mixed deciduous forest (Brownfield Woods: see Vestal and Heermans, 1945: 131, "number of trees as a criterion of plot size"). In this forest the marked numerical preponderance of one species makes the number of trees in the minimum area several times that of a more nearly equable mixture. In comparing mixed types with one-species types, there is reason to believe that the reference area Ar or "smallest representative area," only one-fifth the size of Am or minimum area, is more nearly comparable to the size adequate for a single-species type. If this is true, 101 trees for Brownfield, 20 to 25 trees as a minimum for a simpler or equable mixture, and perhaps fewer than 10 for a pure stand, are equivalent in determining the sizes that are adequate in degree of information provided by one sample plot.

Here may be interjected a recommendation for various types of silvicultural research, from a publication by Munns and others (1935: 9): "As a general rule, a plot should be of such size that at the end of the experiment it will contain at least 100 trees of the predominating age-class."

The foregoing statements apply only to types dominated by woody species in which individuals are readily distinguished. For some grass-dominated types, and for certain herb ground-covers in forest, other characteristics or criteria need attention.

To deal specifically with *Artemisia cana* bush, spacing is close in Test Area 19 of Hanson and Whitman, fairly close in No. 20, rather open in No. 18, the one here treated. The likely plot-size to contain 10 bushes in each of the three stands would approximate these values (in the same order): 3.2, 3.9, and 8.4 milacres, or 13.0, 15.8, and 34.1 sq. m. The smallest plot almost sure to contain one bush is (in Test Area 18) about 2.1 milacre, or 8.5 sq. m.

THE GRASS PHASE. Two views are possible of species-area characteristics of the grassland part of the combination. According to the first view, one regards the grass cover as it is, merely subtracting one species (*A. cana*) from the S-value at any area large enough to include at least one bush. Species-number for 1 sq. m. is reduced by an insignificant amount, from 12.9 to 12.3. A species-area curve would lie just below that for the bush–grass complex: the reference areas would be larger by a trivial amount. The other view is hypothetical, considering the size of reference areas if the bushes were not present, and the grass cover occupied all the area of the terrace. Aside from minor differences in composition, which presumably would make slight or no difference in total number of species, the effect would be to reduce the area required for a particular S-value, in the proportion of space occupied by the bushes, 27.3 per cent. Thus, in place of 12.9 spp. at .247 mlc. and 50 spp. at 11.76 mlc. *with A. cana,* we have 12.3 spp. at .18 mlc. and 49 spp. at 8.55 mlc. without *A. cana.* The curve is displaced to the left, making reference areas significantly smaller: Am is reduced from 11.8 to 8.48 mlc. This effect would be greater in other sagebrush–grass stands if the bushes occupied larger proportions of the total area. Since actual

increases or decreases in the bush part of such dual communities are very common in the West, and since the same relations are found in pastures invaded by shrubs or junipers, or by hawthorn or other weed-trees, or by bushy clumps of cacti, they are of more than hypothetical interest. Reference areas are smaller in inverse proportion to space occupied by the fine-textured phase.

SHORT-GRASS–BUSH MIXTURE, EAST OF BOULDER, COLORADO. VESTAL (1914: 398). This weedy grassland with suffrutices was called the undershrub formation by Pound and Clements, the *Gutierrezia–Artemisia* association by Shantz. It may replace short-grass and other plains grasslands as a consequence of grazing. The particular area studied is a rocky terrace-remnant 4 miles east of Boulder. Its north end was covered with weedy grass cover with many small bushes of *Artemisia frigida,* commonly considered a herb, and *Eriogonum effusum.* (A photograph of this vegetation is shown as Fig. 9 in the article cited). *Gutierrezia* was much less common, but was the conspicuous dominant in the larger area south of a fence which enclosed the north end. The north part had not been grazed in the period just preceding the time of study (Sept. 1913). Other perennials of growth-form other than herbs were *Opuntia polyacantha* and *Yucca glauca.* Estimated density of bushes is 8800 per acre. Four grasses, *Bouteloua gracilis, Agropyron Smithii, Sitanion brevifolium,* and *Stipa comata,* covered 35% of the surface, but much of this cover seemed dead. Conspicuous herbs were *Psoralea tenuiflora, Artemisia canadensis, Chrysopsis, Grindelia, Sphaeralcea, Lithospermum, Boebera,* etc. — A general census of the north part was supplemented by details in 5 1-sq.-m. quadrats, separated. Analysis of data gave species-numbers for bushlets and for herbs in six plot-sizes. Treatment of this mixture differs from the preceding (*A. cana* plus grass) in two respects: there are enough "woody" species to serve for a species-area curve for the bush phase; and the grass phase is treated as it is, not as it would be if bushes were absent.

A result of this treatment of the grass phase is that its Am value (8.13 mlc.) is higher than that for the combination (7.14 mlc.). The composite curve is a simple summation of curves for the two phases.

BUSH–SHORT-GRASS MIXTURE, SAN LUIS VALLEY, SOUTHERN COLORADO. RAMALEY (1942: 260-263, TABLES 5-7). The bush part has been briefly mentioned earlier under the name *Chrysothamnus–Gutierrezia* bush. The whole mixture is xeric and open, with usually somewhat more than half the surface bare. Ramaley gives three tabulations, one for 3 1-sq.-m. quadrats near Villa Grove at the north end of this large intermont plain, one for 50 0.1sq.-m. plots in San Luis Hills (south end), one for 4 4-sq.-m. quadrats on black lava west of Capulin (southwest border of the valley). In the Villa Grove plots, a ground microphyte, the lichen *Parmelia molliuscula,* covers 13% of surface.

THE CHRYSOTHAMNUS–GUTIERREZIA BUSH PHASE. Three bush species lead in both Villa Grove (VG) plots and in San Luis Hills (SL) plots. They

are *Chrysothamnus* sp., *Gutierrezia diversifolia,* and *Opuntia polyacantha* (included with the bushes). *Artemisia frigida,* here a low bush, is in 2 of the 3 VG plots. Only *Chrysothamnus* occurs in the Capulin plots. In extensive areas of this community, most of the following species are found: 1 or 2 large-growing *Chrysothamnus* species, less frequent than low *Chrysothamnus* bushes of 2 to 5 species; *Gutierrezia; Artemisia frigida, Yucca glauca, Senecio spartioides,* 1 or 2 small-bush species of *Eriogonum, Eurotia lanata, Atriplex canescens.* Bushes cover 15 to 25% of the ground. The estimate for ground-space per bush is 0.214 milacre, with 4673 bushes per acre. Data are hardly sufficient for a species-area curve, but one was tentatively drawn from a small-area point, 0.6 spp. at 0.128 mlc., nearly parallel to the curve for sagebrush (the neighboring and similar community of San Luis Valley, with mostly the same bush spp.) This tentative curve gives Am value 27 mlc., Sm 5.73 spp., as compared with 44.7 and 5.30 for sagebrush, which has larger bushes.

THE SHORT-GRASS PHASE. Blue grama grass, *Bouteloua gracilis,* is the only leading species in all three of Ramaley's localities. Herbs are so few in the SL plots that these plots are not used in this species-area treatment. The grass phase is much the same as short-grass of the Great Plains. The number of grass and herb species is considerable (Ramaley lists about 56), but one might need to examine 5 to 10 square miles to encounter so many. In any one locality, species are relatively few. Some of the more frequent species are: *Muhlenbergia Torreyi, Stipa comata, Sporobolus* sp., *Sphaeralcea coccinea, Hymenoxys floribunda,* and *Senecio Fendleri.* Locally frequent are species of *Carex, Comandra, Eriogonum, Potentilla, Astragalus, Lupinus, Gilia, Oreocarya, Chrysopsis, Grindelia.* — The VG plots are considered normal for the type; in them herbs cover about 22.3 sq. decimeters per 1-sq.-m. plot. In the lava near Capulin (LC plots), there is practically no soil; plants grow in crevices, and herbs cover only 41 sq. dm. per 4-sq.-m. plot. The effective size of LC plots is thus nearer 2 sq. m. than 4. Species-numbers are thus available for 2 small plot-sizes, and for aggregates of 2, 3, and 4 plots. Average no. of spp. per 1-sq.-m. plot (VG) is 4.0; per 2-sq.-m. plot (LC) is 3.25. Herb spp. in the 3 VG plots: 5, of which 3 are grasses. Herb spp. in 4 LC plots: 7, including 4 grasses. One-piece areas equivalent to the aggregates ranged from 0.618 milacres for 2 1-sq.-m. plots to 3.56 mlc. for 4 2-sq.-m. plots. For larger areas, 18 species are estimated to require 21 mlc.; 35 spp. to require 800 mlc. — The reference areas found from the curve are very large (Am is 125.5 mlc.). This may be explained by the large amount of bare surface (usually 50% or somewhat more), by occurrence of bushes in the same area, and by the poor representation in both individuals and species of grassland plants other than *Bouteloua.* It is notable that in this mixture the minimum area for bushes, 27 mlc., is much smaller than that for the herbs.

CHRYSOTHAMNUS–GUTIERREZIA PLUS SHORT-GRASS. As in the example of short-grass plus small bushes on the stony terrace east of Boulder, a composite curve for this bush–grass combination of San Luis Valley may not be with-

out meaning. Simple addition of grass and bush species-numbers at particular areas gives a basis for the composite curve. The resulting Am value, 100.8 mlc., is considerably smaller than that for grass alone.

BUSH–GRASS GARIGUE: ERICA MULTIFLORA FORMATION, SOUTHERN FRANCE. C. RAUNKIAER (1916:234, TABLE 3). The bush phase of this mixture was included with other Mediterranean shrub types in Table 9. Raunkiaer listed in 50 0.1-sq.-m. plots 8 low-shrub spp. and 34 others. Of these 34, 10 are regarded as bushes, 24 as herbs. Considering all woody species as comprising the bush phase, their occurrences in plots total 202, making 4.04 species per plot. Grasses and herbs have 141 occurrences, thus 2.82 spp. per plot. The most frequent shrub or bush spp. are *Erica multiflora* and *Fumana procumbens,* each in 34 plots, *Thymus vulgaris* in 25, *Rosmarinus officinalis* in 23, *Helianthemum polifolium* 19, *Genista scorpius* 14. In spaces between bushes are the grasses and herbs. Occurrences for the six most frequent of these are: *Festuca ovina* 28, *Trinia dioica* 12, *Aphyllanthes monspeliensis* 11, *Stipa juncea* 10, *Hieracium pictum* 9, *Asperula cynanchica* 8. Lower scores for these than for woody species result not only from their subordinate status in the complex, but also from Raunkiaer's method of counting all those plants whose crowns overlap the plot. Effective plot-size is thus larger for the larger plants. It is estimated as 0.7 sq. m. for bushes, and 0.2 sq. m. for herbs. The one-piece area equivalent to the aggregate is also separately estimated for the two phases: 14.96 mlc. for bushes, 5.44 mlc. for herbs. Two points can be plotted for the curve of each of the two phases: the curve drawn for grass is regularly higher than that for bush. Ratio of species-number varies little from small to large areas. — Species-numbers for the composite curve were obtained at six areas by simply adding S-values read from grass and bush curves at those areas.

CREOSOTE-BUSH DESERT, COACHELLA VALLEY, CALIFORNIA, AND GILA VALLEY, ARIZONA. H. L. SHANTZ AND R. L. PIEMEISEL (1924: 733-745). *Covillea glutinosa,* now usually called *Larrea divaricata,* is the dominant shrub of this most extensive type. It is the usual vegetation on well-drained desert surfaces, especially rocky outwash slopes or bajadas. The authors studied it in Coachella Valley north of Salton Sea, and near Chandler, Arizona, between Gila River and its tributary, Salt River. The only common woody associate of *Larrea* in these districts is *Franseria dumosa,* a bush ragweed with bur fruits. One shrub (*Krameria Grayi*) and 7 bush species are the other woody plants of the type in Coachella Valley (CV) ; one shrub (*Zizyphus* or *Condalia lycioides*), and 1 bush (a *Lycium*) are the others in Gila Valley (GV). Herb cover consists mostly of spring annuals; it varies greatly in density and in composition from spot to spot and from year to year. Common species are *Plantago erecta, Baeria chrysostoma, Pectocarya penicillata, Amsinckia Menziesii,* and *Thelypodium lasiophyllum.* The lists of common or frequent herbs include 23 spp. for CV and 20 for GV. Of less frequent or rare herbs, 35 are given for CV, 21 for GV.

The two 100-sq.-m. quadrat-maps shown for woody plants include only one species, *Larrea*. A map of the herbs in 1 sq. m. is shown from near Chandler, recorded in late March, 1915. It includes 11 herb species. It is presumed that the same area may later have had a few more species (after the summer rains). In CV this would not be likely. — Plot-map analysis was used to find species-numbers for small areas; these data were supplemented by very rough approximations for large areas. Sample figures, some of which were read from the species-area curves, are as follows:

Creosote-bush: Species-Numbers at Certain Areas.

		0618 *mlc*	.247 *mlc.*	10 *mlc.*	100 *mlc.*	1000 *mlc.*
Woody species:	CV	——	——	0.56	2.18	4.67
	GV	——	——	0.73	1.56	2.55
Herb species:	CV	11.1	16	33.2	42.1	49.0
	GV	10.1	14	30.0	38.0	43.8

In reviewing reference-area findings, the Am values for woody species are very large (530 and 1908 mlc.) as compared with other examples of shrubby vegetation. This is attributed to the open spacing, as well as to the relatively great scarcity of individual bushes of species other than *Larrea* and *Franseria*. The difference between California and Arizona desert shrub examples is pronounced. The S-curve for GV has a feeble gradient (only 4 woody species are listed for the vicinity of Chandler), and its rate of species-increase falls off much more rapidly than that of the CV curve.

The statements of Forrest Shreve (1942:205-207) as to minimal areas in desert vegetation-types are of interest here: In nearly pure stands minimal area is determined by the spacing. In mixed stands [probably much denser than these creosote-bush examples] the minimal area is often not more than 100 sq. m. In rich stands the minimal area must be enlarged to a 500-meter square.

As to the herb populations of the desert floor in CV and GV, their Am values are comparable to those of fine-textured grasslands. The ground-space in few places is so fully occupied that any of the species are excluded by competition of other species from an area larger than a few square feet.

ADDITIONAL MIXTURES. In addition to the conspicuously heterogeneous examples of vegetation just examined, some of the others for which only one curve was prepared may deserve further study, with separate curves for different layers, phases, or components. Almost any stratified forest, and the sclerophyll oak woodland, which shows marked discontinuity (true of many open woody types properly called woodland rather than forest), thus qualify as complexes. The *Sideroxylon* thicket is three-storied. The *Philippia* heath has semi-open top layer of shrubs, with lower ground-cover of several unlike growth-forms. Certain Mediterranean shrub and bush types should be studied in the field as complexes. They represent many combinations of unlike growth-forms. The same

is true of heaths, particularly those with tall-shrub dominants. In heaths, open forests, and in bogs, dwarf-shrub dominants are intermingled with grasses, herbs, and microphytes in innumerable combinations. The *Vaccinium–Dryas* heath with herbs (on Mt. Njulja) is a good example, less complex than some others. The generally complex composition of grasslands is not sufficiently realized: Regel's emphasis upon inequalities of make-up of his *Festuca rubra* meadows is similar to Jaccard's pointing-out of conspicuous differences in "composition florale élémentaire." Most prairies are patchworks or mosaics of diverse elements. However, to the extent that they are not too greatly different in stature and bulk, these unlike elements may be treated together in species-area studies. As grasslands extend into semi-arid countries, suffrutescent herbs and low bushes become more numerous, and may require separate examination as a bush phase. Another growth-form in some tropical grasslands is that with greatly thickened underground woody stem or xylopodium. This may be one of the dominant growth-forms over great expanses, as in Portuguese West Africa, but plants with xylopodia or xylorhizae are commonly an element in mixed tropical grasslands.

Among the elements of bogs here studied, one or another form of *Oxycoccus* (cranberry) mingles freely with sedges where other dwarf-shrub elements are absent. The *Chamaedaphne* bog reported by Kenoyer appears to be notably heterogeneous. The communities developing on rocky surfaces seem to be accidental assemblages of elements from diverse sources. Some of these communities might be like the Boulder mesa-top in requiring separate treatment for unlike parts. Even the lichen communities may be heterogeneous, as in the Howenstine talus, with rock *Cladonias* and also smaller *Cladonias* on fallen logs and branches.

In the author's opinion, frank recognition of the diversity of composition of most communities is desirable. More and more students of vegetation are willing to concede the fact of diversity and the reality of the units of composition, whether these are called synusiae, components, elements, constituents, or something else. A fairly recent tendency in Europe to suppress the term synusia, and to use instead the term society, seems to the writer to be a backward step. Society (as used in Britain and America) is more like the term facies, and is applied mainly to species other than the dominants. To say that a unit of composition should be called by a name that emphasizes an *appearance* (because of local or temporary conspicuousness of one or several species) is indefensible. It not only quite unnecessarily obscures an important characteristic (that the synusia is a unit of *composition*) but it spoils the term society, which should continue to mean a group or layer or seasonal aspect of a community, usually conspicuous in its appearance.

ANIMAL COMMUNITIES AND ASSEMBLAGES

By animal assemblage is meant a part of a community, such as nesting birds within a forest. Results for a very few groupings of animals which have been

studied suggest that their species-area relations are amenable to methods used for vegetation. The species-area curves seem to be of S-form, and reference areas may be found in the same manner. Results from the first two examples are:

	Am	Sr	Sm	D
Sea-bottom fauna, Thisted Bredning, Jutland	3.32 sq. m.	10.0	14.35	2
Apterygota, oak-forest mold, Switzerland	101.7 sq. cm.	9.65	14.6	2

SEA-BOTTOM, THISTED BREDNING IN LIMFJORD. C. H. JOH. PETERSEN AND P. BOYSEN JENSEN (1911, TABLE 1). In this classic study, "The Valuation of the Sea," the two authors reported results with a bottom sampler from different bodies of sea water. Limfjord is the branching passage with alternate straits and *brednings* which crosses northern Jutland. Thisted Bredning is about 21 km. long, 4 to 7 km. wide, and in most parts 10 or 11 meters deep. Its shallow margin has a well-developed zone of *Zostera.* In October of 1909, and April and October of 1910, the bottom was sampled at 100 stations: the animal populations are larger during spring. Table 1, summarizing the first set of 100 samples, was used for a species-area curve. The sampler used in 1909 took in material from 1346 sq. cm. of bottom (0.0333 mlc.). The 3 sets include 35 spp. or closely-similar groups of two or several species. Table 1 includes 25 spp. or groups. The most abundant species are *Ophioglypha* sp. (a brittle-star); the lamelli-branchs *Pectinaria belgica, Nucula nitida, Solen pellucidus, Mya truncata;* the gastropod *Philine aperta;* nereids, etc. Though the basis for estimating one-piece areas equivalent to plot-aggregates was slight, species-numbers were found for aggregates of 2, 4, 10, and 25 plots. For two sizes smaller than 1 plot, random spotting on a map of 4 plots gave likely species-numbers. Some of the species-numbers and one-piece areas used for plotting are:

Area, mlc.	.0037	.0333	.439	1.546	4.85	25.0
Species	2.65	6.85	11.0	14.33	16.5	25.0

The fit of curve to points is not very good. The Am value 3.32 sq. m., or 0.821 milacres, is about that of a fine-textured grassland (e.g., Daubenmire's *Agropyron–Poa secunda* type in Garfield Co., Washington: Am is 0.779 mlc.).

APTERYGOTA FROM FOREST SOIL, AIRE-LA-VILLE, KANTON GENF. H. GISIN (1945). The "plot-size" for study of the ▓▓▓ rthropods was 70 sq. cm., since samples of that extent were remov▓▓ ▓▓▓ the surface soil. (The depth was ca. ·5 cm., volume of sample ⅓ liter. Samples were from 4 localities separated by intervals of ca. 5 meters, with 3 samples from each of the first 2 localities, 1 each from the others. Gisin summarizes his findings in a table, which excludes 5 spp. (some young individuals and a large *Tomocerus,* incompletely known). The table shows for each of 17 species its occurrence in the respective samples, and also its degree of abundance. Gisin decided that over half of the species are *sehr stetig* (8 of them occur in all 8 samples, and 1 occurs in 7). The most abundant species are *Folsomia quadrioculata, Pseudosinella duodecimpunctata,*

Onychiurus armatus, and *Isotomiella minor.* Since the average ⅓-liter sample yielded 78% of all the species found in the 8 samples, Gisin concluded that the *Minimalraum* is not far from the one-sample size. — To prepare an S-curve, mean numbers of species for 1 plot, for 2 neighboring plots, and for 3 neighboring plots were found. If these means are slightly reduced to correct for the somewhat smaller number of species in locality 3, we find that the average for 1 plot is 13.50, for 2 plots 15.46, for 3 plots 16.69. Using Gisin's total of 18 species for 8 plots, we have 4 points, which prove to be all on the convex section of the curve. However it seems clear that the Am value is in the same order of size as Gisin's Minimalraum. His is 70 sq. cm.; from the curve it is 101.7. Gisin considers it essential to study numerous samples of Minimalraum size.

STREAM FISHES, CHAMPAIGN COUNTY, ILLINOIS. D. H. THOMPSON AND F. D. HUNT (1930). The authors emphasize area relations in several ways. Since habitat-complexes vary with size of stream, ten classes are distinguished in a geometric series according to area of the drainage basin above the point of collection. Drainage area, being constant, is a more convenient criterion than volume of flow. The ten area-classes are: 0.5-1 square miles, 1-2, 2-4 . . . 256-512. Tables 1 to 7 show for particular groups of fishes how a progressive increase in number of species accompanies increase in stream size. (A smoothed graph was made showing number of species of all groups plotted against logarithm of area: it has the S-form, but is not comparable to the usual species-area curve.) — The authors had so designed the field study that larger areas of stream were seined in the places representing larger area-classes; number and extent of collection-areas, and consequently also the extent of aggregate collection-areas, were separately recorded for each of the ten size-classes. This is like choosing a graduated series of plot-sizes for work with land vegetation, and makes it possible to apply similar species-area treatment to the data. Figures on p. 15 of the article by Thompson and Hunt show for each drainage-area class the number of collections, the area per collection (in square yards), and the total area seined. The total number of species collected in each drainage-area class had been found from Tables 1 to 7. These totals vary from 10 species from stream-points of smallest area-class to 54 species in the ninth area-class (128-256 sq. miles). Class 7 has 46 spp; class 10 has 42 spp. The entire list from all area-classes numbers 70 spp. — Mean numbers of species per collection were found from the interesting graph by Thompson and Hunt, their Fig. 6, p. 42. It was also necessary to estimate the one-piece area which is equivalent in no. of spp. to each aggregate of well-separated collections (the total collection area). When this was done, species-area curves could be made. (Each is based on only two points, and is thus of low dependability.) — It seemed that results could be of more general import if data for successive drainage-area classes were first smoothed. This was done graphically. Smoothed data for 5 of the 10 classes are tabulated here, with collection areas converted to milacres.

Drainage area sq. miles		Av. area per coll., mlc.	Av. no. of spp. per coll.	Total coll. area, mlc.	1-piece equiv. area, mlc.	Total no. of spp.
1.5	(1-2)	6.28	4.6	60	436	13.6
6	(4-8)	10.2	8.3	148	1078	26.6
24	(16-32)	15.3	12.0	236	1740	36.7
96	(64-128)	19.9	14.7	290	2139	43.0
384	(256-512)	23.0	16.6	333	2450	47.6

Champaign county does not have large enough streams to show whether collection points with drainage areas exceeding 512 square miles would continue to yield progressively greater numbers of species. In the following table of results from the five species-area curves drawn, Am-values are in milacres and square meters as in previous tables; also in square yards, to permit direct comparison with collection areas as given by Thompson and Hunt. All curves and results have Dependability 3.

TABLE 25. Stream Fishes, Champaign County, Illinois.

Drainage area, sq. miles		Am, mlc.	Am, sq. m.	Am, sq. yds	Sr	Sm
1.5	(1-2)	75.0	303.4	363	7.17	10.7
6	(4-8)	168.5	682	815	13.9	20.5
24	(16-32)	242.5	981	1172	19.0	28.0
96	(64-128)	310	1254	1500	22.4	32.8
384	(256-512)	318	1286	1538	24.4	35.8

Since collections are from different streams, and habitats are not usually homogeneous at one collecting point, each line of the table represents a composite of fish assemblages. Because different streams have their faunistic peculiarities, species-numbers in the table are higher than will be found in a given stream at any one station.

It remains to consider possible application of Am values to future stream samplings. Present field methods cannot usually reveal the number of species in a predetermined area of stream so large as the minimum areas given in the table. One can, however, with greater economy of effort utilize the seining method of Thompson and Hunt. One can use known or tentative Am values in estimating how many collections to make in nearby and similar parts of a given station, and how large the collection-area should be. Thus for a station of 6-sq.-mile drainage area, one might require the number of species in an Am of 815 sq. yards. The smoothed value of the area per collection for this stream-size had been found to be 49.4 sq. yds. If this were a plot in land vegetation, 6 such plots somewhat separated (say by 6 plot-diameters) would be equivalent to a one-piece area of 919 sq. yards. (The area-multiplier for this number of plots and interval of separation has been tentatively found to be ca. 3.1. 3.1 × the aggregate area, which is 6 × 49.4, equals 919.) Since this is larger than required, the collection-area can be reduced in the ratio 815:919, making it 43.8 sq. yards. For this and four other stream sizes the figures are tabulated herewith. The multi-

plier for 5 somewhat separated plots is 3.05. Areas (except those of drainage basins) are in square yards.

Am, Converted to Number and Size of Collection-Areas.

Drainage area sq. miles	Required Am	Trial coll.-area	Collections required	One-piece equiv. area	Adjusted coll.-area
1.5	363	30.4	5	463.8	23.8
6	815	49.4	6	919	43.8
24	1172	73.8	6	1373	63.0
96	1500	96.2	6	1789	80.7
384	1538	111.5	5	1700	101

REVIEW OF SPECIES-AREA FINDINGS

MAGNITUDE AND RANGE OF REFERENCE AREAS
FOR DIFFERENT TYPES

The principal numerical results from species-area curves for various communities, already shown in Tables 2 to 24, can be viewed together in Table 26, which combines similar communities into groups. For each group, mean value and also the size-range of minimum areas are shown. A few examples which lie outside what seems to be the ordinary range of sizes are omitted, as well as some others with very uncertain values, such as the Pernambuco and Lagoa Santa forests. Five types are each represented by a single example; 11 groups by fewer than 5 examples. Most of the grasslands are included in groups made up as nearly as possible according to vegetational and geographic similarity. The Buena Vista example was put with plains and mountain-border rather than with mountain types. European and west-American mountain grasslands were put together, leaving European lowland prairies and meadows as a separate group. The grasslands were also segregated arbitrarily into five size-groups according to mean value of minimum area. Two sand-prairie examples with Am >45 were omitted. Readers should have no difficulty identifying most groups with the respective series or parts of series of types shown in Tables 2 to 24, except tropical forests, in which similar types were put together from different parts of the world. The mixed rain forests were put in two groups for which the basis of differentiation (quality of stand and site) is inadequately known. If these 24 examples are combined in one group, its mean Am is 7935 mlc; mean Sm is 86.4; mean N1000 is 179.4.

An even simpler view of the gamut of sizes for vegetation-units is provided in Fig. 5, which shows graphically some of the groups of Table 26. This is supplemented by the selection of representative species-area curves shown together in Fig. 6.

TABLE 26. Summary of Means and Ranges of Minimum Areas for Particular Groups of Communities.*

No.	Description of group	N	Mean Am	Am range		Mean Sm	Density
1	Lichen communities	6	0.10	0.0235–	0.14	12.9	
2	"Most compact" grasslands	7	1.44	0.70–	1.99	21.2	*?40 000*
3	"Medium compact" grasslands	13	3.59	2.00–	4.99	37.1	*?10 000*
4	Columbia Basin prairies	6	4.59	0.77–	12.6	24.9	
5	European grasslands, excl. mts.	9	5.34	1.63–	15.1	42.9	
6	Dwarf-shrub in bogs	5	6.62	0.77–	21.6	10.6	
7	Mountain grasslands	13	6.68	1.74–	16.5	45.8	
8	"Medium coarse" grasslands	12	6.79	5.00–	8.99	44.1	*?2 200*
9	Plains & mt.-border grasslands	8	7.21	1.10–	16.2	27.8	
10	Mediterranean bush types	3	?7.78	6.65–	10.0	?10.2	
11	Moss-layer of bogs	4	8.61	5.00–	12.6	6.99	
12	Grasslands in general	55	9.93	?0.70–	44.9	38.7	
13	Prairies, interior N. Am.	7	10.4	6.30–	17.9	57.4	*(2 022)*
14	Mediterranean shrub types	4	?12.2	6.50–	27.7	?9.12	
15	"Coarse" grasslands	15	13.3	9.00–	17.9	46.7	*?1 250*
16	*Vaccinium—Dryas*—herbs	1	14.9	–		27.9	
17	Sand prairies	7	19.4	13.00–	44.3	31.1	*(103)*
18	Sedge bogs (field-layer)	5	22.3	1.16–	100	13.3	
19	"Open, sparse" grasslands	8	26.0	18.00–	44.9	33.8	*?250*
20	Bush types, Colorado	5	27.9	2.77–	46.0	4.38	3 985
21	Dwarf-shrub heaths	7	43.1	21.3 –	103.2	13.9	
22	Bracken-Blueberry	8	58.3	47.7 –	73.7	40.2	
23	Herb ground-cover in forest	8	67.8	43.1 –	81.7	29.7	
24	Dwarf-shrub g.-c. in forest	7	71.0	49.0 –	107	21.3	
25	*Sideroxylon* thicket	1	92.4	–		69.0	15 520
26	California bush types	2	135	134–	136	12.0	?5 510
27	*Philippia* heath	1	164	–		28.0	8 920
28	Shrubs in forest	2	169	143–	195	8.2	
29	Chaparral types	8	186	56–	450	18.0	(3 215)
30	Oak woodland, sclerophyll	1	319	–		8.7	
31	Mt. forests, low-latitude	3	511	280–	764	18.3	561
32	Young conifer forest	1	519	–		12.1	
33	Ground vegetation under teak	7	707	484–	910	57.3	
34	Old-growth pine forests	2	769	678–	860	8.7	314
35	Less-mixed deciduous forests	6	1 092	718–	1 800	9.0	314
36	Desert shrub *(Larrea)*	2	1 219	530–	1 908	2.6	
37	Mixed deciduous forests	19	2 185	868–	4 015	16.9	192
38	Subtropical & mid-mt. forests	3	2 291	1 575–	3 441	64.6	612
39	Tropical secondary forests	5	3 926	1 320–	5 585	112.8	318
40	Tropical mixed r. f., good	16	6 753	3 890–	11 550	91.2	189
41	Heath forests, trop. lowlands	3	7 603	6 265–	10 000	82.7	216
42	Tropical mixed r. f., fair	8	10 297	5 592–	19 500	76.7	160
43	Tropical river or swamp forests	2	16 183	10 715–	21 650	75.4	154

* Minimum areas (Am-values) are in milacres (1 mlc. = 4.04687 sq. m.). Sm is the number of species at minimum area. See text for statement of communities or stands excluded. Groups are in order of mean Am-values. N is the number of examples in each group. Densities for certain grasslands, in italic figures, are numbers of plants per milacre; for certain shrub types or forests, ordinary figures represent numbers per acre. The diameter-limit for trees is 3 inches. A number in parentheses is not the mean density for a group, but is based on only 1 to 4 examples. Densities for the five grassland size-groups are very rough estimates.
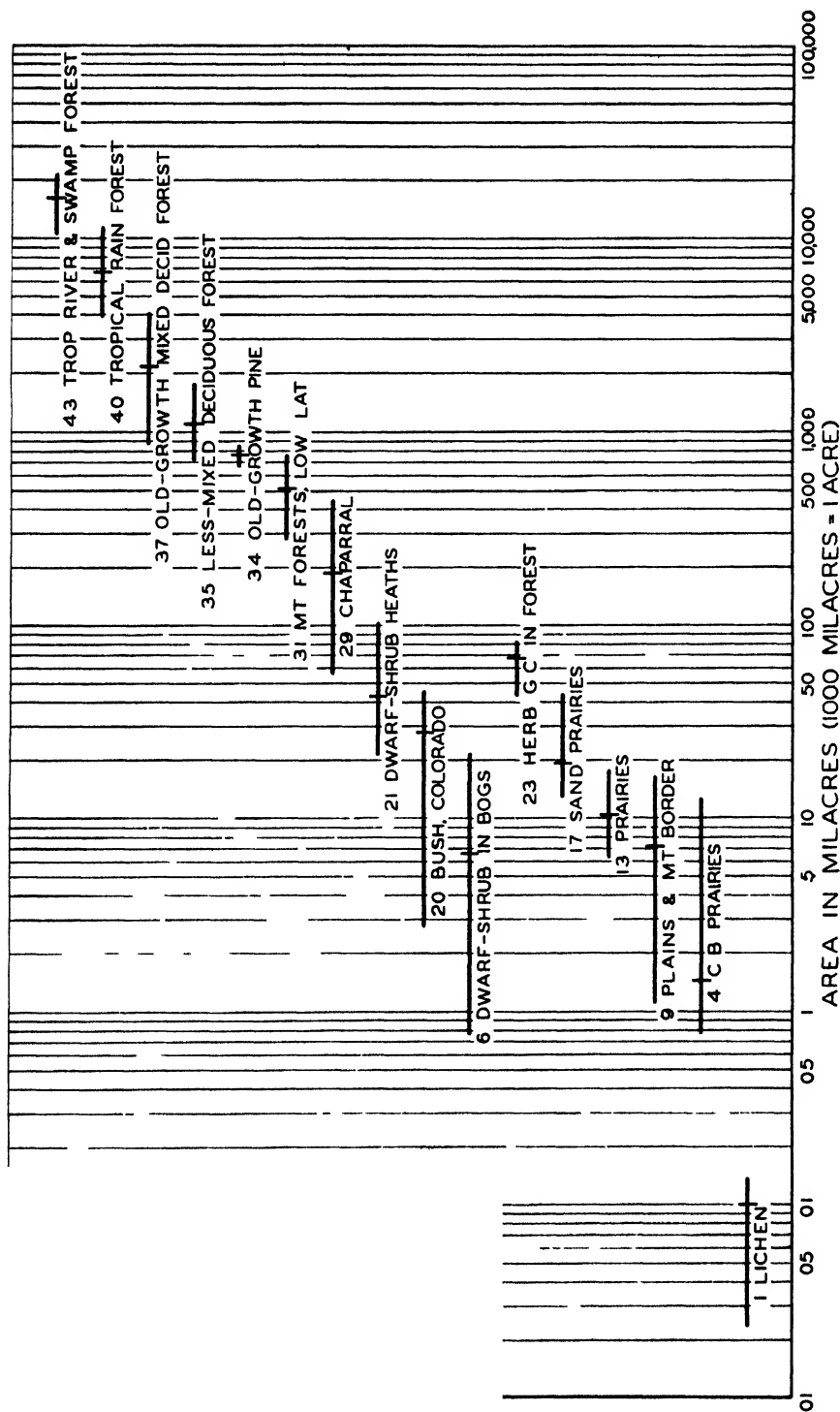
FIGURE 5. Graphic representation of ranges of minimum areas for groups of communities selected from Table 26. Positions of mean minimum areas (mean Am values) are also shown. Numbering of groups is the same as in the table, which shows numerically these same size-ranges and means. Microphyte and herbaceous communities are near the bottom of this figure; bush and shrub vegetations in the middle; forests above and to the right.

AREA IN MILACRES 1000 MILACRES = 1 ACRE

NUMBER OF SPECIES
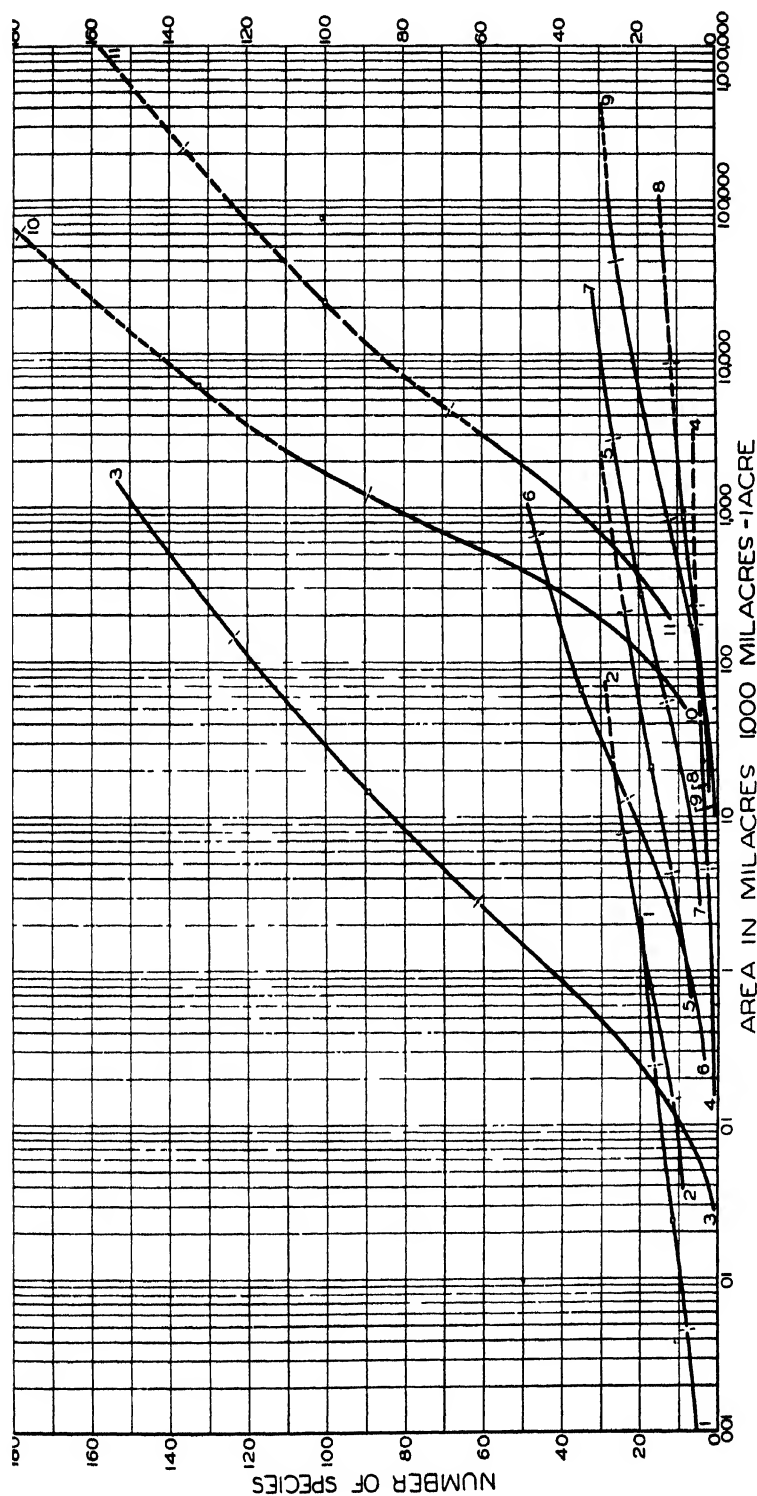
FIGURE 6. A procession of species-area curves for eleven communities. All are drawn to the same scales. The curves for all but three floristically rich communities are thereby much flattened as compared with the original curves, each drawn to a vertical scale appropriate to its own number of species. Further information on the communities represented by the numbered curves will be found in the preceding section.

No.	Description	Am, m/c.	Sm
1	*Lecanora deusta* association of smallest lichens	0.0235	11.7
2	Compact grassland: *Agropyron–Poa.* Garfield Co., Wash.	0.779	17.7
3	Prairie rich in species: *Sporobolus-Andropogon.* N.D.	14.3	89.3
4	Heath with few species: *Calluna* at Østerhede, Jutland	22.0	3.66
5	Relatively rich heath: *Dryas* on Mt. Njulja, Lapland	21.3	16.9
6	Herb ground-cover under forest. Antrim Co., Mich.	65.8	34.4
7	Chamise–sage chaparral, base of Mt. Lowe, Calif.	274	14.6
8	Old-growth white pine, Vilas Co., Wis.	860	8.4
9	Old-growth mixed forest: Brownfield Woods, Ill.	4 015	18.3
10	Primary rain-forest, Kamerun: Johann-Albrechts Höhe	6 065	132.6
11	Mora forest of stream-borders, British Guiana	21 650	100.7

THE GEOMETRY OF S-CURVES

Imagine a "standard S-curve," with reference points R, M, and F at smallest representative area Ar, minimum area Am ($=$ 5 Ar), and area of "fair-sized stand" Af ($=$ 50 Ar). The species numbers at these areas are Sr, Sm (which for present purposes can be put at 1.48 Sr), and Sf ($=$ 2 Sr). The coordinates of the three reference points can be shown in positions which suggest those on the curve, thus:

$$\text{Af, Sf}$$
$$\text{Am, Sm}$$
$$\text{Ar, Sr}$$

We can readily perceive the differences between two curves, or the effects of changing a standard curve, if simple numerical values are assigned:

$$5000, 20$$
$$500, 14.8$$
$$100, 10$$

1. If species-numbers at the stated areas are increased in the same ratio (say 3/2), the curve is made steeper, and reference areas are not changed:

$$5000, 30$$
$$500, 22.2$$
$$100, 15$$

Reducing species-numbers by a constant ratio makes the curve less steep, and similarly does not change reference areas.—Changing species-numbers by a constant increment, as by raising the curve 2 species at all areas as large as 100, makes it necessary to compute new reference points. The new reference areas will in this case be smaller.

2. A shift of the whole curve to right or left increases or decreases all three reference areas in the same ratio, and does not change species-numbers. A shift to right through a distance representing the logarithm of 1.5 gives these coordinates:

$$7500, 20$$
$$750, 14.8$$
$$150, 10$$

3. If it is assumed that the flex point is at R in the "standard curve," consider the effect of changing the curve so that flex point is now above R. On a "standard" graph, the flex point was moved up on the curve from (100, 10) to (160, 11.5). On the readjusted curve (lower part moved upward and leftward), the

changed reference points were found by trial and error, with Sm read from the new Am(= 5 Ar). They are:

$$4480,\ 19.78$$
$$448,\ 14.48$$
$$89.6,\ 9.89$$

Reference areas and species-numbers are reduced, the degree of convexity between R and F is less, and the ratio of Sm to Sr is correspondingly reduced from 1.48 to 1.469.

4. If a curve is made steeper or less steep (as by rotating it on one of the reference points) what are the effects? In a trial operation, a standard curve was pivoted on F and rotated clockwise, raising its lower part until the point that had been R was at 92, 11; and what had been M was at 476, 15.47. To readjust the lower section, the convex part was extended downward to a new flex point at 50, 9.08; and a new concave section was fitted to the curve. New reference points were found, as follows:

$$3000,\ 19.28$$
$$300,\ 14.3$$
$$60,\ 9.64$$

The operation made the curve less steep, and the effect is, as in the preceding case, to make reference areas smaller. The new R is in this instance above the flex point, and convexity between R and F is more pronounced, as shown by the ratio of Sm to Sr, which is now 1.484.

If rotation on R or on M had similarly made the curve less steep, reference areas would likewise have been reduced from original values. If rotation on any point between R and F makes the curve steeper, the reference areas become larger. If the upper part of the curve is raised or shifted to the left, reference areas likewise become larger.

5. Reducing the convexity of the upper section of the curve (with no change in the lower section) makes the upper part steeper, and has the effect of moving the reference points upward on the curve. Conversely, greater convexity moves the reference points downward, giving smaller reference areas with fewer species.

One can usually judge by casual inspection of two curves, considering position to right or left, steepness, and degree of convexity, which of the two is likely to have the larger reference areas. We may now consider some characteristics of communities which affect the position and form of curves and thus the size of reference areas. Thus larger plants yield a curve that is farther to the right; floristic richness makes higher and steeper curves; persistence of rate of species-increment into large areas makes a smaller degree of convexity, steeper upper section, and larger reference areas.

FACTORS INFLUENCING THE SIZE OF REFERENCE AREAS

1. SIZE OF PLANT INDIVIDUALS OR CLUMPS. This is the leading influence in determining extent of reference areas. We should expect lichens or mosses to form the smallest self-contained units of land vegetation; old-growth forests with giant trees, the largest. The community with the smallest lichens does in fact have a smaller minimum area than any formed of larger lichens, and there is a gap between lichen communities and the finest grassland. (The smallest minimum area found for any grassland is 0.48 mlc. for Gilomen's alpine Caricetum mucronatae. This value is not used in Table 26 because of its uncertainty, but the possibility of its being even smaller than 0.48 is not questioned.) As seen with results from the Danish Maglemose, moss-clumps in bogs may be so large that reference-areas have little relation to the small size of individual moss-plants.

Importance of some of the other factors may be gauged from these facts: Although Am for a mixed deciduous forest with giant trees (some reaching 50 inches d.b.h. or larger) may be only 2.5 acres (2761 mlc. in Cox Woods), and possibly as small as 1.5 acres in old-growth mixed conifers, yet the largest Am-value found in tropical forest with perhaps smaller tree-sizes, is over 21.5 acres. This spread, probably more than ten-fold, is due to factors other than size of plants. It is likely that some of these factors work in the direction of reducing rather than increasing minimum area.

2. MARKED DOMINATION BY ONE OR A FEW SPECIES. It is apparent that if the dominants occupy 95% of the space in one stand and 80% in a nearby similar stand, it should take about 4 times as large an area in the first stand as in the second to give equal representation of additional species. Concrete illustrations were encountered in this study. Thus, in Burchardt's tropical forest on Fernando Po, 2 top-story and 2 understory species have 197 trees of the given count of 237. Its Am is slightly larger than the mean for 7 richer West African forests having on the average over 4 times as many species (Am 5690, 5628; Sm 29.6, 127.7).—In the bush near Mt. Lowe, *Artemisia californica* and *Eriogonum fasciculatum* strongly dominate. In an Am of 134 mlc., only 6.9 spp. occur. The larger but more equably mixed shrubs of oak chaparral have an Am of 79 to 262 mlc., with 19.7 to 22.6 spp.—Of the herb covers under shady forest, that dominated by *Anemone nemorosa* under beech at Jonstrup Vang has an Am so much larger than the usual range for the group (116 mlc. as compared with 81.7, next highest) that it was omitted from Table 26.—The *Carex lasiocarpa* bog in northern lower Michigan has an Am of 100 mlc., many times as great as any of the other 3 sedge bogs studied.

3. LOW DENSITY. Scatteredness or wide spacing of individual plants has the same effect as actual size, increasing the area required for sufficient representation of a community. Examples described earlier include the culled mixed deciduous forest at Robinson, Illinois, the grassy parang of Mindoro, the blowsand and some other sand-prairie examples, and the desert shrub of *Larrea*.—High density

works in the other direction. Conditions which tend toward greater numbers of small individuals will be mentioned with other factors.

4. QUALITY OF SITE. Degree of productiveness of a habitat works in several different ways to influence size of reference areas. The very poorest or most highly specialized sites may permit occupation by only one or a few species, with usual requirement of large area for adequate representation of less abundant species. Some of the poorer heaths and bogs, rocky areas, sterile sandy lands, tropical heath forests or wallaba forests, and salt flats with *Sarcobatus*, etc., may be recalled.

The least favorable climates may give the same result, with relatively large reference areas considering the sizes of plants and the numbers of species capable of growing in the area. Here may be mentioned semi-arid bush communities, again the desert shrub of *Larrea*, the mountain forests of low latitudes. But poor climate may not prevent the development of quite rich communities, as the *Vaccinium–Dryas* heath with herbs on Mt. Njulja, above the Arctic circle.

In general the best sites (soil and topography) are more likely to be rich in species and to have relatively small reference areas, although the somewhat below-optimum sites may surpass them through such a set of circumstances as the following: Among Jentsch's primary Kamerun forests, the stand at Ngong-nkeng (Plot VIII) is richest in species (see Table 6). It has 162.2 spp. on 5592 milacres. Of five other primary stands, two (at Mujuka and Bekili) have smaller reference areas, but have many fewer species on these areas. If we use density of tree individuals as a criterion of site quality (it is well known that on better sites competition results in bigger and thus fewer trees per acre), we find highest density in the Ngongnkeng stand, 251 per acre (3″ diam. limit). Density for the five other stands is 136.5 to 242.9 per acre, with the mean at 187.3. The mean Am for the five stands is 6556 mlc., larger than for No. VIII. The 6556 milacres may represent a usual minimum area for good quality West-African forest. The probably inferior stand at Ngongnkeng has richer mixture of species and smaller minimum area partly because its site is less favorable and its trees smaller and more numerous.

5. EXTENT AND FORM OF SITE. A small or narrow area of a particular habitat surrounded by site conditions favoring other kinds of vegetation may have fewer species of its own community and a larger infiltration of species from its neighbors than would the same-sized area within a large expanse of its own kind. Several examples in this study may be cited: the narrow alluvial flat in the Verdugo hills, covered with bush but with strong infusion from neighboring chaparral hills; Potzger and Friesner's ridge-top forests, with rather rich complement of tree species from neighboring slopes of different exposures; Jaccard's Pierrier de Sandalp, a narrow pebbly bench; river-edge forests, such as the mora type as described by Davis and Richards; narrow bluffs or ridge-slopes, as the greenheart type of the same authors. The effects on reference areas are not usually simple, but to the extent that exposure to infiltration from other types

favors continued rate of species-increment at large areas, the reference areas are larger than they would be otherwise. This is obviously the case in the Verdugo Hills flat and the Pierrier de Sandalp.

6. ENVIRONMENTAL DIVERSITIES. JACCARD was probably the first to explain that strong differences of substratum and of topography, notable in certain mountainous districts, are accompanied by similar diversities of floras and of vegetation-units. The total flora of a district, as well as the strictly local flora of any moderately homogeneous area which is not too unfavorable to a majority of the species within range, should be richer because of this environmental diversity. The usual effect upon species-area characteristics of a stand in such a district is probably to increase somewhat the reference areas, but to increase the numbers of species at those areas in a higher ratio.

Diversities within a site, caused by microrelief, rocky ground, and the strong contrasts incidental to much-dissected surfaces (most strikingly described by SKOTTSBERG in one of his accounts of Juan Fernandez), cause the development of complexes rather than uniform associations. Although more species are present on an acre or hectare, the effects on reference areas are not easy to comprehend. It is usually expedient to study separately each of the more important synusiae or phases or layers. Comparison of each of these with its closest equivalent in a nearby homogeneous setting has not thus far been attempted, but should help toward the understanding of a complex.

7. DEGREE OF COMPLEXITY OF A COMMUNITY. It is necessary only to mention that a community regularly possessing two or more layers or phases will have more species, and perhaps on that account requires greater area for their adequate representation than a simpler one-layer community. Reference areas for a particular phase or layer may be larger because of discontinuity of that phase or layer, due to the occupation of space by other parts of the community.

8. FLORISTIC RICHNESS. In itself, the presence of large numbers of species on one homogeneous area has a limited effect in increasing minimum area. In several groups of related communities, curves drawn on the same sheet show great differences in steepness, some with 5 or 6 times as many species as others, but with small differences in size of reference areas. It is true that the physical space-requirements of the greater number of individuals to give a greater number of species, in accordance with the hollow-curve principle, make the minimum area of a highly-mixed forest or prairie larger than that of a simple mixture; but as intimated, this effect is limited. It is greatly exceeded by the effect of floristic richness, not so much of a particular stand or sample area, as of the district and region. It is this richness, of what statisticians would call *the supply* (of additional species), which is chiefly responsible for the often mentioned persistence into large areas of the rate of species-increment. Its effect on the curve is to reduce convexity between R and F (as well as above F), and so to shift reference points to high positions. Grassland and tropical-forest floras of certain regions may thus each constitute a rich supply of species for many of their communities.

9. PROPORTIONS AMONG SPECIES. This may seem to be the same topic as degree of domination, but among dominants as well as among other species there are great differences in proportions. These are most readily seen in the hollow-curve type of graph, in which the species are shown in successive positions, each species represented by an ordinate showing its numbers in a specified area, its frequency of occurrence in plots, or some other quantity. Some J-shaped curves of this kind are deeply hollowed. In a more nearly equable distribution, the leading few species are not so greatly more numerous than the next ones; the curve is not deeply hollowed; many species occur in a small total of individuals (the α-value, or index of variability, is high at the area to which the curve applies); reference areas for the community are small and species-numbers at those areas are high. Some heath, bush, and chaparral communities may show a hollow curve in which the 2 or 3 leading species occur with smaller than usual disparity of numbers, but in which a considerable gap exists between these and the other species, and possibly also there is much disparity of numbers among the others. Such a community will have a large minimum area. The characteristics of communities and their stands which the hollow-curve type of graph may reveal are often explainable, and deserve attention in future studies of vegetation.

10. STAGE OF DEVELOPMENT OF COMMUNITY. A young even-aged forest stand may have one, a few, or many tree species, depending on opportunities for invasion from surrounding areas, as well as on development from sprouts or from seeds in the ground before destruction of the earlier stand. Competition may eliminate species present at first, or new species may enter as time goes on, or both of these may happen. Changes in richness therefore must be studied separately in each stand as it develops. However, without any actual change in the composition of a stand, it is likely to have smaller reference areas if its trees are young and closely spaced.

Similar considerations will usually apply to other types of communities. If the three grasslands at Maalov Krat could be interpreted as three stages of a uniform development (not a safe procedure), reference areas become smaller between one and eight years after the fields are permitted to revert to weeds and to the herbs and grasses from nearby meadows and from the Markskellene (the unplowed border strip, relatively undisturbed and stable). If after some further years of development, the grassy fields become quite like the Markskellene in composition and in texture, they should similarly have reference areas much larger than in the one-year field. One can imagine the vegetative spread of grass-mats and of certain dicot herbs, which increases the average ground-space per plant and so tends to enlarge the reference areas. During these same years numerous additional species enter, giving, as in the Markskellene, a large Sm-value. (Details are seen in Table 17 and the description just following it.)

11. CONDITION OF STAND. Areas showing differing degrees of interference by man or by grazing animals, or different conditions in the same stand at various times, require evaluation in their effects on size of reference areas and

in richness of composition. Usually the effects are cumulative, in the direction of deterioration, and of reducing the number of species, perhaps until only a very few opportunist species remain. Natural causes, as fluctuations within the rainfall cycle, or prolonged immunity in certain places from over-grazing or from fire, may also affect condition of stand. Changes in density may often be easiest to evaluate.

IMPLICATIONS OF CERTAIN RESULTS

The most useful application of findings as to size of reference areas will probably be in selection of sample-plot sizes, in many types of applied ecology; forestry, range ecology, soil conservation, etc. Comparisons of the numerous types of communities studied and of the different examples in any one group may suggest trial plot-sizes which further experience will later modify. While economy of sampling will continue to require the use of many small separated plots, it is recommended that at least one sizable one-piece area be investigated also, to the extent of obtaining a reasonably complete census of species present. This should be as large as minimum area, or if practicable, ten times minimum area (the size of Af). In this way, materials will accumulate for an understanding of the still too little known differences between composition as shown by an aggregate of small plots or by line or strip survey, and that of a sizable one-piece area.

The writer has been repeatedly impressed by the value of definite and comprehensive sets of plot data, especially when essentials for individual plots are included, as can often be done in relatively small space. Maps of quadrats and larger plots are particularly useful. These source materials can be of great value in many ways that are quite unpredictable. Definiteness of statement as to size-limit of trees or plants included, and as to size of area surveyed in an Aufnahme or in a listing of species present, is especially recommended.

There is a growing list of useful botanical descriptions of little-known vegetation-types in many parts of the world by observant collectors and by experienced systematic botanists, foresters, geographers, and other travelers. If, in as many such descriptions as practicable (as well as in articles by ecologists and geobotanists), a definite account can be given of the content of a stated homogeneous area representative of its type, their value will be greatly increased. It may be possible to give a supplementary list of additional species seen in a larger specified area of the same type. Precise identification is not required for all species.

On the whole, the reference areas tentatively determined in this study have proved to be smaller than was expected. As several times mentioned, the Am-value or minimum area seems to be rather conservative, in that it includes more than is usually required for minimal area or Minimiareal by different investigators. If this is so, Af or one-fifth the Am size may prove to be sufficient for many purposes. But as suggested in an article by Richards on tropical forests

(1945), it is not to be expected that in highly-mixed types, different sizable areas will be closely alike in composition, particularly if they are well separated. This is true even if the areas are several times as large as Af, the "fair-sized stand," equal to 10 Am.

One implication of this small size of reference areas may be of use in efforts by biologists and conservationists to preserve areas of natural conditions and remnants of vanishing types of plant cover with their animal inhabitants as well. So far as plants and smaller animals are concerned, a preserved area as large as 1 to 10 Am is truly representative of its type. Even in old-growth forest with Am values up to 4 acres in deciduous mixed types and up to 10 or 20 acres in tropical mixed types, an area of Am size is worth preserving. It is true that the smaller the area, the greater are the hazards to which even its further study by investigators may subject it. The preservation of several small areas instead of only one may reduce the hazards. It is easier to see that a surviving prairie remnant no larger than 5 to 15 milacres is worth preserving, if we know that this size may exceed the minimum area. Again, as with tropical forests, the more numerous such remnants can be, the better, since no two need be expected to be closely alike. A 10-milacre prairie might have such dimensions as 5×8.1 meters, or 17.4×25 feet, or 20×21.8 feet. It is even possible to reconstruct a sample of a desired type of grassland. A "synthetic" prairie (or other vegetation) could be established where it might be desired, in park, museum ground, botanical garden, or university study-plot, by transplanting, seeding, and for a considerable period, weeding by hand. A small, carefully-tended sample of natural or synthetic vegetation is better than a large one which cannot be maintained.

Another implication of the usually small size of reference areas may bear on problems of classification of natural units of vegetation. Various students of vegetation have quite different opinions as to the extent and degree of unity of plant associations, and as to the number of kinds of natural units that should be recognized and named. The smaller the areas required to exhibit the characteristics of types, and the greater the variations shown in these small areas, the more likely it is that there are very large numbers of types, readily distinguishable and in many cases worthy of recognition. The minimum extent of a stand is suggested by the size of reference areas for a type. The minimum extent of the aggregate of all stands referable to one type is similarly pertinent to this problem of the extent and number of associations or other vegetation units. The writer has collected much information bearing on the problem. An abstract of a preliminary presentation (at St. Louis, March, 1946) may be found in *Bull. Ecol. Soc. Am.* 27 (1) : 15.

The close relations between species-area studies and the problems of floristic richness are ably treated in Richards' article on tropical rain forest (1945). The present study has brought to light some complications in the definition and expression of such indices of floristic richness as the Mischungsquotient (mean number of tree individuals per species). This index is not wholly adequate; of

several tropical forests, No. 1 may be richest by one standard, No. 2 by a second, and No. 3 by a third. Materials toward clarification of such standards were accumulated in this study, but do not belong in the present report.

HYPOTHESES TO EXPLAIN SPECIES-AREA CURVES

This subject is closely connected to the next one, the need for additional studies. As the reader will have concluded, the principal need in further elucidation of species-area relations, whatever system of coordinates is used in showing them graphically, is rational explanation, with incorporation of important factors into an equation for a species-area curve. There is no reason to doubt that considerable progress in mathematical parts of the problem will be made before long. Those interested will find much of value in the articles by Romell (1920, 1923, 1925, 1926, 1930), Brenner (1921), Svedberg (1922 a and b), Nordhagen (1923), Kylin (1923 a and b, 1926), Wicksell (1924), and Teräsvuori (1927). (The last includes valuable materials which should be further analyzed.) Three assumptions of Romell (1930: 591) are considered to be especially likely to lead to further mathematical insight. Romell states: "The only theoretical curves which . . . check satisfactorily with empirical findings . . . seem still to be those deduced from a *normal curve of variation* (or rather a set of such curves), making three simple and clear assumptions. . . . Every one of the species is adapted to a definite site; . . . the site factors in the area or district analyzed vary from point to point according to pure chance around a mean value; . . . on the average it is just as probable to have species adapted to the rarer combinations of site factors as to those commoner in the particular area." The third assumption is amplified in a footnote. It may not be superfluous to recall a fourth (which may be implicit in Romell's first): each species is more or less plastic: it has an amplitude of toleration above and below a mean value representing the "optimum" of each factor affecting it. Whether these assumptions are sufficient for communities exhibiting strong competition is another question to be considered.

Two other mathematical approaches may be suggested. Both are based on the hollow-curve principle. One is the investigation, already well advanced, of Fisher's series dealing with numbers of species in relation to numbers of individuals. (See Fisher, Corbet, and Williams, 1943; and Williams 1944). This series makes use of the number of what may be called the "tail-end" species: those which in a given collection (of insects, in most of the materials reported) are represented by a single individual. Empirical hollow-curve findings from plot data for vegetation (encountered in the present study) suggest that fewer plant species are represented each by one individual than one would expect from Fisher's series. As earlier intimated, established populations of rooted plants appear to be influenced by factors additional to those affecting the insect materials studied by Corbet and Williams.

An empirical approach to the understanding of the properties of hollow curves

might consist in the construction of a graduated series of such curves from new field data for each of several different kinds of vegetation. Each plot will yield its own hollow curve for numbers of individuals of the different species present. The normal character of a curve for a given plot-size can be determined from study of many curves for individual plots of that size. If the normal curve for each plot-size of a graduated series is thus found for a particular vegetation, and if the study is repeated for different vegetations, materials for other types of· mathematical analysis of hollow curves will be available. The form of empirical hollow curves for plant communities will probably depend more upon leading species than upon tail-end species. "Degree of hollowness" will be slight in equable mixtures, pronounced in communities showing strong domination by one or a few species. Further information on hollow curves will be found in the article by Fisher et al. (1943) and in works there cited. Earlier emphasis on hollow curves is well known through the writings of J. C. Willis. See Willis and Yule (1922); Willis (1940). A paper by J. C. Chamberlin (1924) is notable.

A mathematician may perceive further points of attack upon species-area problems from the writer's hypotheses to account for the nearly straight and the obviously convex sections of S-curves. Consider first the small-area end of a curve for forest. It was expected that at a plot-size equal to average ground-space per tree (N or mean number of trees per plot $= 1$), the mean species-number, S, would also be 1. But some plots of this size have 2 trees; in half or more of these plots both trees belong to the most abundant species; and other plots have no trees. On the average, S is slightly less than 1 when $N = 1$, so far as present experience indicates. Similar considerations apply to types other than forest.

The tail of the curve, if much prolonged into smaller areas than that at which $N = 1$, approaches zero. In the other direction the concave section of the curve becomes steeper as far as the flex point. The concavity is a consequence of plotting area on a logarithmic scale, since the S/N ratio decreases progressively from the smallest areas onward. Curvature is slight in the vicinity of the flex point, which means that species-increment continues at nearly the logarithmic rate expressed by the slope at the flex point, up to a plot-size at which convexity of the curve becomes apparent.

Persistence of fairly rapid rates of species-increment from small areas to beyond the flex point may be explainable from the following considerations: (1) Even in fairly homogeneous sites there is perceptible variability of site conditions from spot to spot, as stated by Romell. Some of this is due to basic physical diversities of soil or of surface; some is due to plant or animal reactions, as in shading by bushes or in spotty occurrence of decaying stumps or of animal burrows. (2) There is also a partially independent variability of plant cover due to vagaries of plant distribution. It results partly from chance location of the spots which individuals of any species were able to reach and to colonize, partly from aggregation by local seeding and vegetative spread. (3) The space-scales

of these environmental and plant-location diversities vary, partly with sizes of plants, partly otherwise. In some communities the mosaic of variabilities is predominatingly fine-textured, in others coarse-textured but in any community there are both large-scale and small-scale inequalities of environment and of plant cover. Romell's 1930 paper shows clear recognition of the existence of a prevailing texture of variability. A sufficiently coarse texture makes the vegeta-·tion a complex rather than an association. Romell states (p. 593) : "At least very often, the 'homogeneity' . . . consists of a sufficient 'regularity' and a sufficiently short 'wavelength' of the recurring variations in the composition of the plant cover, rather then in a thorough mixing of the elements of the vegetation so as to form a uniform carpet. . . ."

The rapid increase in species-numbers at very small areas is due to addition of space for enough individuals to represent more than the one or two species first included. After the two or three commonest species are present, the next increments are due to variabilities of plant cover. As more and more kinds of the smaller pieces of the mosaic, and later as larger pieces are included, more and more species are represented in the area attained. Variations· of the general pattern are still being added at areas some distance beyond the flex point. At an area at which convexity of the curve has for some distance been apparent (about at Am or minimum area), the common variations have already been included; beyond Af further additions are chiefly of rare species. Only a rich supply of additional species from surrounding territory, or the encountering of new and different variations of site and of plant cover, will determine a curve which ascends with little convexity into strikingly large species-numbers. Although the different sections of a species-area curve are more readily visualized if the area scale is logarithmic, the above considerations apply also to curves plotted to two linear scales. On these curves also, reference points can be found by trial and error.

ADDITIONAL STUDIES NEEDED

Of particular species-area problems in need of further study, new field data for communities of few species should settle the already-mentioned questions whether some curves fail to yield twice as many species at fifty times the area, and whether some heaths and bogs may have "double curves." These, if found, may show initial ascent of the curve through areas smaller than one square meter, to a nearly level section with very small increment of species, succeeded by a second steeper section of the curve as less common species are included. (See the account of Russian bogs). Study of impoverished communities in which an absolute limit in species-number may be reached (at least for certain stands) should also be made. These show a "curve of saturation," in which, as in one curve for same flats with *Sarcobatus,* the upper section is a horizontal line. Some of these, if large-enough areas are available, may be found to have "double curve

Certain kinds of vegetation whose species-area relations are practically unknown include two-phase grass-and-tree combinations, open forests, tropical grasslands, Mediterranean and Californian grasslands, South African grasslands and those of temperate South America; most types of vegetation in Australia and New Zealand; Amazonian forests, mountain forests in South America; moss communities in bogs, on cliffs and other rock surfaces and on tree bark; desert communities. Many types of temperate forests, especially of conifers, have received little attention. Direct comparisons of shrub or of ground layers in different forests will be improved if field data for species-area purposes are obtained in the same manner.

As to improvement of field methods in species-area studies, one can recommend: determination of species-numbers in larger and more numerous one-piece areas of graduated sizes; if practicable, determination or estimation of density as well as of species-numbers; in forests, use of 7-cm., 3-inch, 10-cm., or 4-inch diameter-limits, with provision of data for dependable conversion from the limit used to any of the others; more general construction of plot-maps; and study of at least 50 plots of the smallest size chosen (these have greatest variability in species-number and in other characteristics). More general publication of plot-maps and of data for individual plots is also highly desirable.

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THE MORPHOLOGY AND PHYLOGENY OF
AUCHENORHYNCHOUS HOMOPTERA

The
Morphology and Phylogeny
of
AUCHENORHYNCHOUS
HOMOPTERA
(Insecta)

By
SOL KRAMER

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CONTENTS

INTRODUCTION

Comparative studies of insect structure and resulting classifications based on phylogeny have been few in comparison to the amount of material available for study. Handlirsch (1906-08) was able to establish the minimum geologic age of many groups of insects through paleontological studies, and he considerably modified the prevalent conceptions of his day concerning the ordinal relationships of insects. Although Tillyard (1930), Carpenter (1930), and others have attacked this problem, fossil insects are meager in comparison to other animal fossils and many gaps still exist in this line of evidence. Consequently, the insect taxonomist must depend on morphological, physiological, ecological, and zoogeographical sources for his evidence of insect relationship. It should be added that the vast numbers of insect species and groups, ordinarily a handicap, is of decided advantage in phylogenetic studies. Insects have retained in varying degree many primitive characters and their large numbers increase the possibility that there may be derived from existing forms, composite pictures of ancestral types which will clarify relationships.

Just such an attack on the problem of insect phylogeny, through extensive comparative studies of present-day forms, has been made by Crampton (1924). During the past forty years he has undertaken studies of relationship throughout the Insecta, based upon diverse characters, such as the head capsule, thoracic sclerites, wing articulation, abdominal segments and appendages, and genitalia, as well as on the characters of wing venation and mouthparts previously relied upon. His studies, which provided important new concepts of insect phylogeny, have done much to lay the groundwork for future investigation. It should be noted, however, that Crampton's studies were devoted primarily to the broader relationships of insects, and his resulting classification concerns the relationships of the higher categories such as subclasses, superorders, and orders. The problems of phylogeny within the orders of insects, concerning families and lower groupings, remain virtually unsolved.

This comparative study of the Auchenorhyncha is an endeavour to examine one such problem of relationship. One species from each of five families of Auchenorhyncha has been selected for detailed study. Some of the material presented here has been dealt with by others, but much of it is new. Relationships of structure have been indicated by many original drawings, and these studies of the structure of representative Aucheno-

1

rhyncha have for the first time been incorporated into and compared in a single work. The writer has further included a detailed account of the musculature of the membracid representative, *Ceresa bubalus*.

This investigation represents only a preliminary effort toward the understanding of relationships within the Auchenorhyncha. Through it, the writer has been impressed with the little that is known concerning the functional significance of particular structural modifications. Snodgrass (1935), Weber (1933), and others have done a good deal to emphasize the importance of ascertaining the functional value of anatomical facts, and the value, wherever possible, of supplying reasons for existing structures. Such comparative functional studies should be integrated with morphological studies within the lower categories of insects, if we are to approach some understanding of what has been taking place in the evolution of insects. In this connection it would not be amiss to point out that comparative studies of behavior patterns in some groups of arthropods, such as bees, wasps, spiders, etc., have provided valuable characteristics for the systematist. Such work is based on the assumption, as Lorenz (1939) has pointed out, that "the concept of homology, useful in morphology, is just as applicable to inherited behavior-patterns as to bodily characteristics." Sound classifications should be based on the integration and evaluation of all ascertainable phylogenetic evidence.

The large numbers of insect species have in some measure precluded these studies by systematists. It is nevertheless true that the systematist who specializes in a particular group of insects is in the best position to answer such questions, for he is most intimately acquainted with the many species represented and their diverse modifications of structure and behavior. Future attempts to provide reasons for structure, even though our efforts be faulty, will lead the more quickly to an understanding of what has been taking place in the diverse auchenorhynchous groups of insects, and to a greater comprehension of the Homoptera in general. It is hoped that this study will stimulate questions among taxonomists in these insect groups, and will provide some morphological basis for their answers.

NOTES ON CLASSIFICATION

In a work on the general classification of animals, Dumeril (1806) separated the Hemiptera into six families. Two of these families, the Collirostres or Auchénorinques,[*] comprising the cicadas, membracids, cicadellids, fulgorids, and cercopids, and the Plantisuges or Phytadelges, comprising the aleyrodids, chermids, aphids, and coccids, represent in part the Homoptera as we know them.

Westwood (1840), adopting Latreille and Burmeister's view as to the division of Homoptera into three primary sections, named these sections on the basis of differences in the number of tarsal joints as follows:

1. Trimera. Tarsi 3-jointed: antennae minute, setigerous, wings areolate (*Cicada*, Linnaeus).
2. Dimera. Tarsi 2-jointed: antennae moderate, filiform, 5-10 jointed: wings subareolate (*Aphis*, Linn. and *Psylla*, Geoffr.).
3. Monomera. Tarsi 1-jointed: antennae 6-25 jointed: wings not areolate (*Coccus*, Linn.).

The Dimera contain the families Psyllidae, Aphidae, and Aleyrodidae; the Monomera contain the Coccidae; while the Trimera contain the Cicadidae, Fulgoridae, and Cercopidae.

Amyot and Serville (1843) in their work on the classification of Hemiptera separated the Homoptera as a suborder, and divided the latter into sections, Auchénorhynques and Sternorhynques. The former section contains the Trimera of Westwood, while the latter comprises both the Dimera and Monomera.

Buckton (1889) grouped the cicadas, membracids, fulgorids and jassids into a single family, Tettigiidae, which he separated from the Aphidae, Coccidae, etc. Following Latreille, who had divided the Cigalles or Cicadae into two groups separating the singing from the nonsinging forms, "les Chanteuses" and "les Muettes," Buckton separated the Tettigiidae into two subfamilies. The subfamily Stridulantia contained the tribes Tibicinae and Cicadinae, while the subfamily Silentia contained the tribes Membracinae, Fulgorinae, Cercopinae, and Jassinae. In this connection it is interesting to note a recent comment by Evans (personal communication, 1948) concerning a broadcast given by Ossiannilsson from Stockholm of the amplified songs of jassids and cercopids, which sounded like the songs of cicadas and frogs. He adds that Ossiannilsson

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[*]This name refers to the apparent origin of the beak or proboscis, from the "neck" or cervical region, as contrasted with the Sternorhyncha in which the proboscis seemingly arises from the prothoracic sternal region.

had previously published a paper (Opusc. entom., 1946; 82) in which he gives a preliminary note on sound-producing organs in the Homoptera. Evans (1946b) had not seen this paper when he called attention to a supposed tymbal in an aetalionid, *Darthula hardwickii* Gray.

Distant (1906) has pointed out that Westwood recognized only three families of Auchenorhyncha: the Cicadidae, Fulgoridae, and Cercopidae. Stal divided this group into four families: Stridulantia, Cercopida, Jassida (including membracids), and Fulgorida, and in this view he was supported by Hansen. Although Distant treats the Membracidae as a separate, fifth family of the Auchenorhyncha, he adds that both Stal and Hansen may possibly be right, on morphological grounds, in relegating the membracids to a subfamily of the Jassidae.

According to China (1927), the family Peloridiidae was erected for a primitive insect *Peloridium hammoniorum* taken on Navarin Island, Tierra del Fuego, described by Breddin in 1897, and assigned to the Heteroptera. In 1924 a new genus and species of this family, *Xenophyes cascus*, taken in New Zealand, was described by Bergroth. In the same year another new genus and species, *Hemiodoecus leai*, taken at Hobart, Tasmania, was described by China.

Myers and China (1929) concluded that the Peloridiidae were more closely allied with the Homoptera. This conclusion was primarily on the basis that the only character clearly separating the Heteroptera from the Homoptera was the presence of the gula, absent in the Homoptera and the Peloridiidae. They suggested a new series, Coleorhyncha, for the Peloridiidae, to be placed at the base of the Homoptera. The classification of Hemiptera, based on key characters, was modified by them as follows:

Gula present .... HETEROPTERA
Gula absent .... HOMOPTERA
    Rostrum arising from base of head
        Base of rostrum sheathed by propleural structures...... COLEORHYNCHA
        Base of rostrum entirely free from prothorax........ AUCHENORHYNCHA
    Rostrum arising between or caudad of fore coxae....... STERNORHYNCHA

More recently Evans (1946a), as a result of extensive taxonomic and morphological studies of the leaf-hoppers and related Auchenorhyncha, proposed a separation of this group into three divisions, as follows:

1. Tegula almost always present; middle coxae elongate, articulated far apart free and capable of lateral movement; hind coxae immobile; wing without a marginal vein...... Fulgoromorpha
    Tegula absent; middle coxae short, articulations near together; hind coxae mobile; wing with a marginal vein.................2
2. Head with a swollen postclypeus, the crown with a small triangular frons bearing a median ocellus........... Cicadomorpha

> Head with a large but not necessarily swollen postclypeus,
> which may or may not be distinct from the frons; frons
> without a median ocellus........................Jassidomorpha

He then subdivides the Jassidomorpha into two superfamilies as follows:

> In the head, the anterior arms of the tentorium fused with the posterior arms; hind coxae short, conical, not transversely dilated; hind tibiae with one or a few spurs but lacking spines ....Cercopoidea
>
> In the head, the anterior arms of the tentorium not in contact with the posterior arms; hind coxae transverse, laterally dilated; hind tibiae armed with spines, some of which may be mounted on enlarged bases.........................Jassoidea
> (includes the Membracidae)

In his most recent study Evans (1948) reiterated his concept that the membracids belong to the jassoid complex, and divided the membracids into three families, the Nicomiidae, Lamproteridae, and Membracidae.

MATERIALS AND METHODS

The procurement of properly preserved and adequate numbers of specimens constitutes a major problem for such a study. Proper preservation, essential for the study of insect musculature, is sometimes obtained by chance when live specimens are dropped into 70 per cent alcohol. But for the most part this method is inadequate. The musculature of some insects used in this study, first dropped into steaming water and then into 70 per cent alcohol, was fairly well preserved. By far the best method of preservation, on the basis of comparative tests with *Ceresa bubalus,* is to drop live specimens into steaming water and then transfer to a 5 per cent solution of chloral hydrate where the insects may be stored indefinitely. Steaming water, followed by Bouin's fluid for 24 hours, then storage in 70 per cent alcohol gives almost equally good results.

A variety of dissecting tools were made by grinding, on carborundum and oilstone, stainless steel, surgical needles into extremely fine points, probes, or scalpels and placing these into lightweight, dental broach holders. A pair of microdissecting scissors, the blunt ends of which were ground down almost to needlepoint, proved very useful.

Dissections were performed underneath 50 per cent alcohol in metal pillboxes, ¼ inch high by 2 to 3 inches in diameter, bedded with paraffin wax. As many as a score of dissections were made for each figured drawing. The drawings were first made on cross-section paper, but later tracing paper, underneath which a cross-section guide had been placed, was used. An ocular micrometer proved to be an invaluable aid for this work.

For the dissection of the smaller insects in this study, an adaptation of a method described by Guyer (1947, p. 92) proved very helpful. Longitudinal, or cross-sections of small insects, or of parts of insects such as the head, thorax, etc. were imbedded in paraffin wax. In imbedding, a small area of paraffin is first melted with a hot needle or scalpel. The section of the insect which has been removed from 70 per cent alcohol, and blotted to remove excess liquid, but allowed to remain moist, is immersed in the liquid paraffin up to the upper surface of the insect section. The paraffin around the insect section is again melted so that it securely grips the section when it sets. The dissecting pan is then flooded with 50 per cent alcohol. Any paraffin which has run into the muscles or other internal parts may be readily picked away with a needle. Dissections of minute muscles and parts, which might have been extremely difficult, were greatly facilitated by the use of this technique.

Another method which was of value in muscle study was an eosin staining and oil of wintergreen clearing procedure which I have recently

6

described (Kramer, 1948). This technique enables one to view the position and relationship of muscles in the thorax and abdomen directly through the body wall of the insect. It was particularly useful when used to ascertain the position of muscles in such smaller structures as the labium, and segments of the leg of *Ceresa bubalus*.

THE SCLERITES, APPENDAGES, AND MUSCLES OF THE HEAD OF AUCHENORHYNCHA

Scolops pungens Germar

(Fulgoridae)

Long considered as a single family Fulgoridae, the fulgorids have more recently been given superfamily rank (Fulgoroidea) and have been considered to represent as many as eighteen families. The modifications of the head in this group are of particular interest since the head has been interpreted by past writers to represent both specialized and generalized modifications in the Homoptera.

The head of *Scolops pungens* is shown in frontal view in figure 7. The median striated area is the postclypeus (pclp), beneath which is the anteclypeus (aclp). The small labrum (lm) is suspended from the anteclypeus, and the lorae (lor) lie laterad of the clypeal area. Above, the frontal region or frons (fr), prolonged dorsally into a cephalic process, is separated from the postclypeus by the epistomal suture (est). The frons contains three ridges or carinae medially and a pair laterally, the latter extend down through the clypeal region. The prominent compound eyes (e), lateral ocelli (oc, Fig. 6) and antennae (ant, Fig. 8) all lie laterad of the frontal region.

The elongate region, posterior to the lorum and anteclypeus is termed the maxillary plate (mxp, Fig. 8). The labium (lb) is suspended by a membrane from the posterior edge of the maxillary plate and the hypopharynx (not seen). Both the lorum and the maxillary plate are separated from the genal region above (ge) by a definite internal ridge which apparently represents the subgenal suture (sgs). The presence of the subgenal suture in this fulgorid, partly present or absent in other fulgorids, is particularly noteworthy. The line separating the lorum and anteclypeus from the maxillary plate has sometimes been referred to as the genal suture, but this is a misnomer since the maxillary plate is merely closely approximated to the margins of the lorum and anteclypeus and is in no way joined to them.

The mandibular stylet (mds), sometimes called mandibular seta, or mandibular bristle, is shown in figure 12. It consists of a comparatively broad basal portion and a narrow bristle-like terminal portion. The retractor muscle (rmds), originating on the vertex of the head capsule, is inserted on the base of the mandibular stylet by means of an elongate tendon. The base of the stylet gives rise to another arm, termed the lever

8

(lvr$_1$), which articulates with the lorum at the point where the subgenal suture meets the epistomal suture. On this lever is inserted the protractor muscle (pmds) which originates on the ventral and anterior margins of the lorum.

The maxillary stylet (mxs, Fig. 15) is likewise broader at the base and narrows to a long terminal bristle. It possesses a long retractor muscle (rmxs) originating on the vertex of the head and a protractor muscle (pmxs) originating on the maxillary plate. A membrane ensheaths the protractor muscle and forms an enclosed lobe with the maxillary plate. The base of the stylet is enclosed in a pouch formed by this maxillary lobe, the hypopharyngeal wing plate (hwp), and the posterior tentorial bridge (tb), but the stylet is actually outside the head capsule. A sclerotized lever (lvr$_2$) runs from the base of the stylet to an apodeme of the head capsule, apparently a part of the posterior tentorial bridge. The muscles and levers of both the maxillary and mandibular stylets are thus within the head capsule; whereas the stylets alone are in pouchlike chambers outside the head capsule. It should be noted that the mandibular and maxillary stylets of this fulgorid each possess single protractor and retractor muscles.

The labium (Fig. 17) appears to consist of four parts. A basal segment invaginates inwardly to form an apodemal process. Beyond this basal segment there are a pair of sclerites on the posterior wall of the labium and these are followed by two long segments. Anteriorly, the labium possesses a groove along its entire length in which the bristles of the mandibular and maxillary stylets lie. Apart from a narrow, median, sclerotized rod, this groove is membranous. Protractor muscles (plb) and retractor muscles (rlb) of the labium, originating on the margins of the hypopharyngeal wing plates, respectively, are inserted on the apex and the base of the apodemal process of the first segment. A median section of the labium (Fig. 14) reveals a pair of muscles (mlb$_1$) going from the paired sclerites of the posterior wall to the median sclerotized process of the anterior groove, a second pair (mlb$_2$) from the median sclerotized process of the groove to the posterior wall, another small pair (mlb$_3$) from the lateral edge of the anterior groove to the posterior wall, and a fourth group of muscles (mlb$_4$) running from the median sclerotized process to the posterior wall.

The hypopharynx is best seen in a median section of the head (Fig. 13). Laterally the hypopharynx sends a pair of chitinous plates, termed hypopharyngeal wing plates, dorsally where they meet the tentorial bridge (hwp, Fig. 9). Muscles (dsyr) originating on the hypopharyngeal wing plates are inserted on an apodemal process of the salivary syringe (syr) which is located in the hypopharynx. A pair of salivary ducts (sld) from

the salivary glands unite to form a common median duct which empties into the salivary syringe. The saliva is discharged through the ventral tip of the hypopharynx into the salivary channel formed by the maxillary stylets which come together at this point.

The dorsal or anterior wall of the hypopharynx forms the posterior or ventral wall of the sucking pump (pmp). As Snodgrass has shown this is not the true mouth but a portion of the preoral cavity termed by him the cibarium. The anterior wall of the sucking pump is formed by the inner epipharyngeal wall of the clypeus. This anterior wall of the sucking pump gives off a series of tendons medially on which are inserted the large dilator muscles (dlclp) originating on the postclyeus.

Of considerable significance are the lateral arms of the hypopharynx (lh) which extend to the loral plates (Figs. 9 and 10). These connecting sclerotized arms between the hypopharynx and lorae are very small in comparison to the broad connection existing in the other homopteran families to be considered.

The tentorial structure consists only of a posterior tentorial bridge (tb, Figs. 9 and 16) extending from the dorsal tips of the hypopharyngeal plates across the posterior opening of the head capsule. Unlike the cicadid, cercopid, cicadellid, or membracid, there is an apodemal connection between the head capsule and this tentorial bridge. In other Homoptera, as far as has been ascertained, the posterior bridge extends across the occipital foramen, but the original connections with the head capsule have been lost. In *Oliarus aridus* (Fig. 11) an actual invagination or tentorial pit (ptp) appears to exist on either side of the tentorial bridge between the hypopharyngeal wing plate and the maxillary plate.

The antenna (Fig. 7) consists of a small basal segment or scape (scp), followed by a large bulblike pedicel (pdc) and a threadlike, single segmented flagellum (fl). Three antennal muscles (mant), inserted on the scape, have a common origin on the tentorial bridge (Fig. 9).

It is interesting to note the various modifications of the postclypeus and the loral areas found in the fulgorids. As indicated previously, Evans, Spooner, and others have considered the loral areas to be lateral modifications of the postclypeus. Figures 2, 3, and 5 show some of these modifications. In these fulgorids the lorum, more or less, completely merges with the postclypeus. Of significance in homologizing this loral area throughout the Homoptera is the fact that the protractor muscles of the mandible always originate on this region of the head however it may be developed, as shown in the lateral views of an undetermined species of *Acalonia* (Fig. 1) and *Ormenis pruinosa* (Fig. 4). This will be a more fully discussed in a later section on phylogeny. *Oliarus aridus* is shown (Fig. 6) to indicate the presence of a median ocellus. A median ocellus is

apparently present among the fulgorids only in the subfamily Cixiinae, and only in the Cicadidae of other Auchenorhyncha.

Tibicina septendecim (Linn.)
(Cicadidae)

Because of their large size, the head and mouthparts of the Cicadidae have been the subject of more studies than any of the other Homoptera, so that this group is fairly well known. Marlatt (1895), Snodgrass (1921, 1927), Myers (1928), Evans (1938, 1940), Butt (1943), and others have made studies of representatives of this family. A description of *Tibicina septendecim* together with additional drawings, however, is included here for comparative study and interpretation.

The most conspicuous feature of the head is the greatly enlarged post-clypeus (pclp, Fig. 19). A strong internal ridge is present medially and it is demarked from the anteclypeus (aclp) by a very definite suture. It is at once apparent that in this respect the head of this cicada has reached a far greater development than shown among the fulgorids. The dominance of the clypeal area in this and the remaining families of Auchenorhyncha is in marked contrast to that found in the fulgorids where the clypeal area, although fairly well developed, occupies a considerably smaller portion of the total head area. The loral areas (lor) extend dorsally almost as far as the postclypeus itself. Internally a strong apodemal ridge (clr, Fig. 25) is present between the lorum and postclypeus. The labrum (lm) fits over the basal portion of the median groove of the labium (lb).

On the dorsal surface of the head (Fig. 26) three ocelli (oc) are present. A median ridge runs from the back of the head to just behind the median ocellus and sends two, somewhat faintly divergent ridges anteriorly. The triangular region (fr) containing the median ocellus evidently represents the frontal area. The anterior dorsal dilator muscle of the pharynx (phym$_1$, Fig. 18) originates on the anterior margin of this triangular frontal area.

The mandibular stylet (Fig. 28) possesses retractor muscles (rmds) inserted on an internal tendon given off by the elongate arm of the base, which go to the dorsal part of the head. Mandibular protractor muscles (pmds) originating on the lorum are inserted on the considerably enlarged lever and apodeme of the stylet. The lever (lvr$_1$, Fig. 25) articulates with the dorsal-most portion of the lorum just below the point where the anterior tentorial arm (at) invaginates inwardly.

The maxillary stylet (Fig. 23) varies considerably from that found in the fulgorid. Instead of one retractor muscle there are now two (rmxs$_1$ and rmx$_2$), with separate insertions on the base of the stylet and sep-

arate origins on the dorsal wall of the head. In addition to the protractor muscle (pmxs) originating on the maxillary plate, the strongly sclerotized lever of the maxilla (lvr_2) also bears a protractor muscle (pmxl) originating on the maxillary plate and a retractor muscle (rmxl) originating on the posterior tentorial bridge.

The labium (Fig. 21) consists of three segments: a basal segment, an expanded middle segment, and an elongate terminal segment. A pair of median protractor muscles (plb) inserted on the apex of the apodemal process and a pair of lateral retractor muscles (rlb) inserted on the basal segment both run to the hypopharyngeal wing plate. A median section of the labium (Fig. 22) indicates that there are three pairs of muscles, one pair (mlb_1) extends from the terminal margin of the first segment to the sclerotized rod and apodeme of the anterior median groove, a second pair (mlb_2) from the sclerotized rod to the lateral wall of the middle segment, and a third pair (mlb_3) from the median rod to the dorsal wall of the middle segment. No muscles were seen in the terminal segment.

The hypopharynx (hph, Fig. 18) contains the salivary syringe (syr) and gives rise posterolaterally to the greatly enlarged hypopharyngeal wing plates (hwp, Fig. 20) upon which the dilator muscles of the syringe lever (dsyr) are attached. The comparative size of the hypopharyngeal wing plates is seen in figure 27. United with the main body of the wing plate laterally is a thin sclerotized plate which appears to be an apodemal process (mxap, Fig. 20) of the maxillary plate. The lever of the maxillary stylet articulates with this apodeme, and not directly with the maxillary plate as has heretofore been figured and described by some writers. These two posterior plates, together with anterior membranes which meet where the dorsal tip of the hypopharyngeal wing plate unites with the lateral extremity of the posterior tentorial bridge, form the pouch which contains the mandibular and maxillary stylets.

The anterior wall of the hypopharynx forms the ventral, cup-shaped floor of the sucking pump. To the roof of the sucking pump, which nests concavely in the ventral floor, are attached the large dilator muscles (dlclp). Contraction of these muscles arches the roof convexly and creates the pressure which sucks the food into the preoral cavity. As can be seen by lifting or removing the anteclypeus, the hypopharynx is broadly joined laterally to the lorae. The tentorium in this cicada (Fig. 25) consists of a posterior tentorial bar or bridge (tb) from which two arms (at) run anteriorly to the anterior tentorial pit (atp, Fig. 19). Each of these anterior arms gives off a dorsal arm (dt), to the apex of which the antennal muscles are attached. The antenna consists of a basal scape, a pedicel, and a terminal threadlike flagellum.

Lepyronia quadrangularis (Say)
(Cercopidae)

The study of the head and mouthparts of this family of Homoptera, aside from that included in the study of the external structure and biology of *Lepyronia quadrangularis* made by Doering (1922), has received almost no attention.

The postclypeus (pclp, Fig. 29) of *Lepyronia quadrangularis* is again characteristically striated. There is no suture separating the anteclypeus (aclp) from the postclypeus as occurs in the cicada, but its distinctness is indicated by lateral indentations. The anteclypeus is elongated ventrally beyond the head capsule over the basal segment of the labium (lb). The labrum (lm) suspended from the anteclypeus lies over the median groove of the middle segment of the labium. Dorsally the postclypeus continues into a quadrangular area (fclp, Fig. 31) in which is incorporated the frontal region or frons. That this quadrangular area represents some part of the frontal region is substantiated by the anterior dorsal dilator muscle of the pharynx (phym$_1$, Fig. 30), which takes its origin from this region. The vertex (vx, Fig. 31) contains a pair of ocelli (oc). The head of *Lepyronia quadrangularis* is actutely angular, when viewed from the side, with the frons and vertex making up the dorsal surface. The ventral surface, comprising the clypeal area and labrum, slants posteriorly (Fig. 30).

The mandibular stylet (Fig. 34) is similar to that found in the cicada. The protractor muscles (pmds) originating on the lorum are inserted on the lever of the mandible (lvr$_1$) and the retractor muscle (rmds) is inserted on the narrow arm of the base of the stylet. The lever articulates with the upper corner of the lorum, but it is situated a considerable distance beneath the anterior invagination of the tentorium.

The maxillary stylet (Fig. 33) is drawn with the protractor muscles (pmxs) of both the base of the stylet and lever (lvr$_2$) enclosed within the membranous sheath of the maxillary plate to show the relationship of these parts. A pair of retractor muscles (rmxs) is inserted on the base of the stylet. The lever also possesses a retractor muscle similar to that in the cicada and in fact the entire musculature of the maxillary stylet is simliar to that of the cicada. The lever of the stylet articulates with the apodemal plate of the maxillary lobe (mxap, Fig. 32) and not to the maxillary lobe itself.

The three-segmented labium (Fig. 37) is comparatively short and thickened. The protractor (plb) and retractor muscles (rlb) are similar to those already described in the fulgorid and cicada. Five pairs of transverse muscles are seen in the basal and middle segments but there are apparently no muscles in the terminal segment.

The mouthparts (Fig. 30) are very similar to those described for the cicada. The salivary syringe (syr), however, is well developed and comparatively large. The dilator muscles of the salivary syringe (dsyr) are of unusual size and are seen to occupy a very large proportion of the posterior head opening (Fig. 32).

The tentorium, as in the cicada, consists of a posterior tentorial bridge (tb, Fig. 32), and a pair of anterior arms (at, Fig. 34), each with a short dorsal arm (dt). The antennal muscles (mant) originate on the apex of the dorsal tentorial arm.

The left half of the head of *Lepyronia quadrangularis*, with the lower part of the postclypeus, the anteclypeus, labium, and labrum dissected away, is shown in figure 35 to reveal the relationship of the lorum (lor) to the hypopharynx (hph). There is a broad ridge, normally covered by the anteclypeus, which joins the lorum to the hypopharynx. This connection between the lorum and hypopharynx is similar to that which is present in the cicada. In addition there exists an internal ridge or apodeme where the lorum and postclypeus meet, termed the clypeal ridge (clr, Figs. 34 and 35).

A cross-section of the head through the sucking pump, stylet pouches, and muscles of the mouthparts is shown in figure 36 to indicate their relationships.

Aulacizes irrorata (Fabr.)
(Cicadellidae)

Evans has made a comprehensive taxonomic and morphological study of this group over a period of ten years and in 1938 provided a valuable evaluation of intrarelationships of this family based on an analysis of their morphological characters. He considers that the external structures of the head are second in value only to the venation of the wings for purposes of comparative studies and the determination of phylogenetic relationships. Although this group is here designated as a family for purposes of uniformity, he considered it to be a superfamily, the *Jassoidea*, and divided it into twenty-one separate families. Later (1948) he reduced the familial divisions to eight, including three families of membracids.

The head of *Aulacizes irrorata* is in many respects similar to the cercopid, *Lepyronia quadrangularis*. The clypeal region, however, is a little larger and bulges out considerably more than in the cercopid. In ventral view (Fig. 38) the large striated postclypeus (pclp), although merged with the anteclypeus (aclp) beneath, is demarked from it by lateral indentations. Laterad of the anteclypeus are the loral regions (lor). The small labrum (lm) fits over the median groove of the short, compact labium (lb). Dorsally the postclypeus merges with the frons to form a frontoclypeal region (fclp, Fig. 39). Although it is not possible to deter-

mine the exact extent of the frons, it should be noticed that the anterior dilator muscle of the pharynx (phym₁, Fig. 40) originates just ventrad of the dorsal surface so that the postclypeus probably does not extend beyond this point. The posterior limits of the frons may possibly be marked by the prominent lateral indentations. The vertex (vx) bears a pair of ocelli (oc). The antenna consists of a basal scape and pedicel and a long threadlike flagellum which shows marks of segmentation basally.

The musculature of the mandibular stylet (mds, Fig. 46) is uniquely different from that of the preceding forms. In addition to the protractor muscle (pmds) running from the lever (lvr₁) to the lorum and the retractor muscle (rmds₁) going from the base of the stylet to the vertex, there is a second retractor muscle (rmds₂) which goes to the anterior tentorial arm (at).

The base of the maxillary stylet (mxs, Fig. 42) has one large retractor muscle (rmxs) which originates on the vertex and a pair of protractor muscles originating on the maxillary plate. One protractor muscle (pmxs) is inserted near the base of the stylet, the other (pmxl) is inserted on the lever (lvr₂). The lever is broadly articulated to the apodemal plate of the maxillary (mxap).

The short, compact labium (Fig. 43) consists of three segments. Two pairs of small triangular plates are present posteriorly on the terminal segment, one pair located basally, one pair apically. Evans (1937) has suggested that these paired plates may represent the glossae and that the surrounding terminal segment is derived from the paraglossae. Likewise, the basal and middle segments may represent the "mentum" and "prementum." These latter terms are of little value, however, for it has so long been the custom to give names indiscriminately to various divisions of the labium that the actual homology of the parts to which such terms are assigned is doubtful. The usual pair of protractor (plb) and retractor muscles (rlb) originating on the hypopharyngeal plates are inserted on the apodemal process and base of the labium. A median section of the labium (Fig. 44) reveals six pairs of transverse muscles.

The parts of the hypopharynx and the sucking pump mechanism are very similar to those parts already described in previous forms. It should be noted, however, that the sucking pump cavity when fully distended is unusually large, and together with the well developed dilator muscles (dlclp) indicates that this form possesses a powerful sucking apparatus.

The tentorium consists of a posterior tentorial bridge (tb, Fig. 41) and a pair of anterior tentorial invaginations (at, Fig. 46) to which the dorsal tentorial arms (dt) are attached. The pair of anterior tentorial arms usually running to the posterior bridge is absent. Instead, where the anterior tentorial arm might be expected there is found the tendon from

which arises the retractor muscle of the maxillary stylet. This tendon may in part be a vestige of the anterior tentorial arm. The dorsal tentorial arm can be identified by the antennal muscles (mant) which have their origin on the apex of this part.

Ceresa bubalus (Fabr.)
(Membracidae)

The head and mouthparts of the Membracidae have been treated in the earlier comprehensive works on the taxonomy, biology, and morphology of this group by Branch (1914), Funkhauser (1917), and Lawson (1922). These have provided very desirable and basic information concerning the Membracidae, but certain inaccuracies exist in these studies because the homologies of the head and mouthparts were not as well understood then as they are now. These works have not provided any consideration of the musculature.

The head of *Ceresa bubalus* is considerably flattened anteroposteriorly. Seen in ventral aspect (Fig. 47) the conspicuous median area is the postclypeus (pclp), beneath which is the anteclypeus (aclp). The labrum (lm), suspended from the anteclypeus, fits over the median groove of the three-segmented labium (lb). The lorae (lor) are located on the sides of the clypeal areas. The postclypeus is continuous on the conspicuous median protuberance of the anterior surface of the head (Fig. 48). At least a small dorsal portion of this protuberance representing the frontal region of the head combines with the postclypeus to form a frontoclypeus (fclp), since the anterior dilator muscles of the pharynx (phym₁, Fig. 49) have their origin here. The vertex (vx), divided by a median ridge, possesses a pair of ocelli (oc). The vertex, which lies dorsally in the previous forms discussed, is anterior in position in a line with the metopidium of the pronotum, while most of the clypeal region, normally anterior, lies ventrally.

The mandibular stylet (Fig. 54) has a large group of protractor muscles (pmds) inserted on the lever (lvr₁) going to the lorum, and three retractor muscles. The first of these muscles (rmds₁) originates on the dorsal region of the head capsule, the second (rmds₂) on the dorsal arm of the tentorium and the third (rmds₃) originates on a lateral internal edge of the hypopharyngeal wing plate where it meets the margin of the head capsule. All three are inserted on the basal portion of the mandibular stylet.

The maxillary stylet (Fig. 53) is greatly elongated and its pouch has been invaginated beyond the tips of the hypopharyngeal wing plates (Fig. 50), so that it is separated from the vertex of the head by a pair of short retractor muscles. There are two protractor muscles originating on

the maxillary plate (mxp), one (pmxs) inserted at the base of the stylet, the other (pmxl) inserted on the lever (lvr$_2$). The lever itself apparently articulates with the lateral edge of the hypopharyngeal wing plate (hwp). It should be noted, however, that the hypopharyngeal wing plate has merged with the apodemal plate of the maxillary (mxap). This makes it appear that in this membracid the wing plate is formed from both the lateral elongation of the posterior of the hypopharynx and an invagination of the maxillary plate.

The three-segmented labrum (Fig. 51) resembles that of the leafhopper *Aulacizes,* in that the posterior surface of the terminal segment bears a pair of almost triangular plates basally. Paired protractor muscles (plb) and retractors (rlb) originating on the hypopharyngeal wing plate are inserted on the apex of the apodemal process and the basal segment, respectively. A median section of the labium (Fig. 52) indicates that four pairs of muscles are present within its three segments.

The hypopharynx (hph, Fig. 49) contains a small salivary syringe (syr), the dilator muscles of which (dsyr, Fig. 50) are attached to the hypopharyngeal wing plates. The sucking pump (pmp) is very similar to those of the previous forms. The epipharyngeal wall upon which the dilator muscles (dlclp) are inserted forms the anterior wall of the pump, while the anterior wall of the hypopharynx forms its posterior wall. The pump leads into the pharynx. It should be noted that the frontal connective nerve from the brain runs anterior to the anterior dorsal dilator muscles of the pharynx. As Snodgrass (1947) has shown, this nerve and its ganglion separates the preoral muscles, which include the dilator muscles of the sucking pump (dlclp), from the postoral muscles, which include the hypopharyngeal muscles and pharyngeal dilator muscles. Behind the brain there are two pairs of dorsal dilator muscles of the pharynx (phym$_2$, phym$_3$) going to the top of the head capsule and a lateral group (phym$_4$) going to the tentorium.

The tentorium consists of a posterior tentorial bar, or bridge (tb), and the short dorsal arm of the tentorium (dt, Fig. 54) which arises from the anterior invagination of the tentorium. The antennal muscles (mant), as usual, have their origin on the dorsal arm of the tentorium. The anterior arm of the tentorium, partly incorporated into the base of the dorsal arm, has otherwise disappeared. The antenna consists of two basal segments, the scape (scp) and pedicel (pdc), and a terminal flagellum (fl).

THE THORACIC SCLERITES, WINGS, AND LEGS
OF AUCHENORHYNCHA

The thoracic sclerites of the Auchenorhyncha, and the Homoptera generally, have received relatively little study. Aside from the general studies of Crampton (1926) and Snodgrass (1927) which contain references to individual Homoptera, the most extensive comparative studies of the thoraces of the Homoptera is that of Taylor (1918). The wings, however, have received better treatment and there exist good comparative studies of the wings of the Fulgoroidea, Cicadellidae, and Cercopidae by Metcalf (1913, 1917a, 1917b) and of the Membracidae by Funkhauser (1913). Myers (1928) has discussed the thorax and wings of the Cicadidae in his comparative study on the morphology of this family.

Scolops pungens

Prothorax. The head is closely joined to the prothorax by the cervical membrane. There are no distinct cervical sclerites present. The prothorax (Fig. 55) consists mainly of a saddle-shaped pronotum which covers the dorsum and extends down over most of the pleural region. The pleural region is considerably reduced. A portion of the episternum (es_1) extends beyond the ventral margin of the lateral lobe of the pronotum, but the epimeron (epm_1) is completely covered. Between these pleural sclerites is the pleural suture (pls_1) which extends into the coxal process (cxp_1), a pleural articulation for the coxa of the leg.

The prosternum (st_1, Fig. 60) consists of a small sclerite connected to the episternum on each side by a narrow, elongated precoxal bridge or precoxale (pcx_1). The trochantin (tn) is a small sclerite which forms a point of articulation for the leg between the episternum and precoxale and the coxa.

A pair of invaginations or furcal pits (fp_1) give rise to a pair of sternal apodemes or furcae (fu, Fig. 63). Each furcal apodeme unites with a pleural apodeme ($plap_1$) represented externally by the plural suture. Together, these sternal and pleural invaginations represent the prothoracic endoskeleton.

Mesothorax. The tergum of this wing-bearing segment (Fig. 56) is composed of several distinct regions, the most conspicuous of which is the large scutum (sc_2). Anteriorly a narrow ridge represents the precosta or pretergite (pte_2). Behind the scutum is a small scutellum (scl_2), the posterior margin of which forms a fold or reduplication (rd_2). This posterior fold of the scutellum continues into the axillary cord (axc_2), forming a

18

connection with the posterior margin of the wing. The postnotum (pnt$_2$) although morphologically a part of the mesothorax is more closely associated with the metathoracic tergum. Laterally it unites with the mesothoracic epimeron (epm$_2$) by means of the postalar bridge (pw$_2$). Anteriorly the prealar bridge (aw$_2$) unites with the episternum.

The dorsal region of the forewing is articulated to the metathoracic tergum by means of a basal membranous area within which are a number of articular sclerites, collectively termed the pteralia. The first of these sclerites, the first axillary (1ax$_2$, Fig. 56) articulates mesally with the anterior notal wing process (anp$_2$) and laterally with the second axillary (2ax$_2$). The second axillary in turn articulates with the common base of the subcosta and radius of the wing veins and with the third axillary (3ax$_2$), while the latter axillary is united with the base of the vannal region of the wing. The basal margin of the vannal region forms a sclerotized fold or lip which fits into a groove formed in the scutellar region of the tergum, locking the wings in place when they are folded at rest.

The pleuron (Fig. 55) is composed of the episternum (es$_2$) and the epimeron, separated by the pleural suture (pls$_2$). Dorsally these areas continue along the pleural suture to form the pleural wing process or articulation for the wing (pw$_2$), while the pleural coxal process (cxp$_2$) articulates ventrally with the coxa. The mesothoracic spiracle (sp$_2$) lies in the membranous region below the prealar bridge.

The membranous ventral area of the wing which unites the wing to the pleuron contains several small sclerites, which serve for the insertion of important wing muscles. These are termed the alaria by Crampton and the epipleurites by Snodgrass. Anterior to the pleural wing process is the basalar sclerite (ba$_2$) united to the episternum. Behind the pleural wing process is a narrow elongate subalar sclrite (sa$_2$) which apparently unites with the postalar bridge.

On the ventral side, the sternum (st$_2$) is broadly joined to the episternum by means of the precoxale (pcx$_2$). The trochantin (tn$_2$) lies between the precoxale and the coxal cavity. A pair of furcal pits (fp$_2$) form invaginations of the sternum which give rise to branched furcal apodemes internally. The lateral branches of these apodemes unite with the pleural apodemes as in the prothorax. The mesothoracic pleural apodeme is considerably developed dorsally and extends into the body cavity just below the tergum.

Metathorax. The mesothoracic scutellum overlies a considerable portion of the metathoracic tergum, and the normal position of the two wing-bearing segments has been displaced in figure 56 to reveal the divisions of the metatergum. As already noted the postnotum (pnt$_2$) belonging to the mesothoracic segment, is closely joined to the prescutum (psc$_3$) of

the metathorax. The antecostal suture (acs_3) which separates the post-notum from the prescutum is the external demarcation of the poorly developed metathoracic phragma. The prescutum is separated from the scutum (sc_3) by elongate membranous areas on each side. The scutellum (scl_3) is poorly developed. Its posterior margin folds over to form a reduplication and continues into the posterior margin of the wing by means of the axillary cord (axc_3). A broad postnotal region (pnt_3) is closely united to the scutellum. The postnotum gives off a pair of narrow arms laterally along the posterior margin of the pleuron to meet on the venter, forming a postcoxal bridge ($pocx_3$). The postcoxal bridge on each side unites with a median triangular sclerite. The apex of this triangle sends an elongate sclerotized process anteriorly between the large membranous area of the coxae, which bifurcates into the body cavity.

The dorsal basal membranous area of the hind wing has a number of articular sclerites. A small first axillary ($1ax_3$) lies between the anterior notal process (anp_3) and the larger second axillary ($2ax_3$). Posteriorly the third axillary ($3ax_3$) articulates with a prominent posterior notal process (pnp_3).

The metathoracic pleuron (Fig. 55) presents a specialized structure, apparently correlated with the development of jumping hind legs. The episternum (es_3), demarked from the epimeron (epm_3) by the plural suture (pls_3), is cleft ventrally by membrane. Both the episternum and the epimeron have been shifted in position so that these sclerites lie almost horizontally, rather than vertically. Consequently the pleural wing process (pwp_3) has been pushed to the extreme anterior point of the pleuron. The coxa has become rigidly united with the pleuron and although the coxa (cx_3) and meron (mr_3) may be broadly distinguished from the episternum and epimeron, considerable comparative study of this region among the fulgorids would be required to determine the exact boundaries of these sclerites. Taylor (1918) has indicated, however, that in species of *Ormenis* and *Fulgora,* a comparable region bears muscles extending to the subalar region, and since such muscles connect the subalar sclerite and meron in other insects he concluded that the region in question is a part of the coxa, and not of the pleuron.

The ventral basal membrane of the wing does not possess an externally visible basalar sclerite anterior to the pleural wing process as does the mesothoracic segment. Posteriorly, however, there is an elongate subalar sclerite (sa_3).

On the venter the sternum is united both to the mesothoracic sternum anteriorly and to the episternum laterally through a precoxal bridge (pcx_3, Fig. 60). A wide membranous area separates the precoxal bridge from the coxae. The origin of the small sclerotized areas within this mem-

branous region is uncertain, but may have been derived from the tro-chantin.

Wings. The forewing is elongate-oval in outline and is somewhat thickened, forming a tegmen-like covering for the membranous hind wing. A vannal fold (vf) divides the hind wing into an anterior remigium and a posterior vannus. The basic wing venation is noted in figures 79 and 80.

Legs. The mesothoracic leg (Fig. 80) consists of a basal coxal segment (cx₂), a short trochanter (tr), the femur (fe), tibia (ti), and a three-segmented tarsus. The tarsus (Fig. 92) bears a pair of ungues or claws (cl), between which is a membranous pad or pulvillus (pu). The basal rim of the coxa is demarked at the basicoxa (bcx) and a small lateral portion forms the meron (mr). The prothoracic leg (Fig. 89) is almost identical to the mesothoracic leg in structure, except that the meron (mr₂) is less developed. The larger metathoracic leg (Fig. 91) is modified for jumping and consists of a coxal segment (cx), the meron (mr₃) of which is rigidly joined to the pleuron. There is a small trochanter, a femur, and a tibia with a posterior row of toothlike spines, and a border of spines apically. The apical ends of the first two tarsal segments are similarly spined.

Tibicina septendecim

Prothorax. The cervical region of the cicada, *Tibicina septendecim,* contains a pair of median dorsal cervicals (dc, Fig. 57) and a pair of lateral cervical sclerites (lc).

Like the fulgorid, the principal sclerite of the prothorax of the cicada consists of a saddle-shaped pronotum which covers most of the pleural region. In other respects, too, it is quite similar, except that there is a postcoxal bridge (pocx₁, Fig. 61) ventrally as well as a precoxal bridge (pcx). In addition, the median sternal region (st₁) is modified into a troughlike structure in which the labium of the head lies in repose.

Mesothorax. The main feature of this segment is that it bears the principal burden of flight of the cicada. As a consequence this segment is greatly enlarged and presents a number of modifications primarily correlated with the flight mechanism. The tergum consists of an anterior prescutum (psc₂, Fig. 57) with the scutum (sc₂) lying posteriorly and laterally. There is a narrow precostal region (pc₁) present anteriorly, which is bent back over the prescutum, and this relationship can best be seen in longitudinal section shown in figure 59. The phragma (ph₂) which is fairly well developed is not suspended vertically, but is directed anteriorly in a horizontal direction and can be seen dorsally beneath the prothoracic intrasegmental membrane.

The postnotum (pnt$_2$), although closely united with the metathoracic tergum medially, is also joined to the reduplication (rd$_2$), or posterior fold of the scutellum (scl$_2$), laterally. The invaginated plate arising from the posterior margin of the postnotum gives rise to a large, well developed phragma (ph$_2$, Fig. 62) upon which arise the powerful oblique dorsal muscles of the mesothoracic tergum. The phragma is thus anchored both to the mesothorax laterally and to the metathoracic segment medially. Four axillary segments, in the basal membranous region of the dorsal surface of the forewing, provide a part of the tergal articulating mechanism.

Laterally (Fig. 58), the episternum and epimeron are respectively divided into upper anepisternal (aes$_2$) and anepimeral (aepm$_2$) regions and below into katepisternal (kes$_2$) and katepimeral (kemp$_2$) regions. Connected to the episternum in the basal membranous area of the ventral surface of the wing is the basalar sclerite (ba$_2$) while the subalar sclerite (sa$_2$) is behind the pleural wing process (pwp$_2$).

The mesosternum consists of a broad basisternum (bst$_2$, Fig. 61) separated from the prosternum by a membranous region, but joined laterally to the katepisterna by precoxal bridges (pcx$_2$). The medioposterior furcasternum (fst$_2$) contains a pair of furcal pits (fp) which invaginate to form the furcal apodemes internally. Postcoxal bridges (pocx$_2$) join the furcasternum to the katepimera.

Metathorax. This segment is considerably reduced in comparison to the mesothorax, and although the hindwing which it bears apparently plays a lesser role in the flight of this insect, it does nevertheless actively enter into the flight mechanism. The scutellum of the mesothorax overlies half of the metathoracic tergum, but the latter has been withdrawn in figure 57 to reveal its parts. To be noted is the fact that medially the scutum (sc$_3$) is separated from the scutellum (scl$_3$) by a membranous cleft. A small postnotum (pnt$_2$) is present behind the scutellum. The basal membranous region of the dorsal surface of the wing contains four axillary sclerites.

Ventrally the basisternum (bst$_3$) is rigidly united with the mesosternum anteriorly and joined to the pleuron by precoxal (pcx$_3$) and postcoxal bridges (pocx$_3$), while the furcasternum (fst$_3$) is posteriorly united with the sternum of the first abdominal segment (I).

Wings. The forewing (Fig. 81) is almost twice as large as the hind wing (Fig. 82) and is apparently the principal flight organ, although as has been mentioned the hind wing is undoubtedly an equally active but lesser organ of flight. This is emphasized since the development and sclerotization of the wing-bearing segments is closely correlated with the degree of activity of both the fore and hind wings. Care must be taken

not to mistake structural correlations with the flight mechanism for phylogenetic relationship.

Attention should be called to the nodal line of the fore wing (nl) which forms a break in the sclerotization of some of the principal vein branches, previously thought to be present only in the Cicadidae. Evans (1948) has shown that a nodal line is also present in the jassoid family, Hylicidae. The basic venation, noted in figures 81 and 82, is well discussed by Myers (1928) for the Cicadidae as a whole.

Legs. The legs of the cicada bear the same segmentation as noted in the fulgorid. The prothoracic leg (Fig. 93) is turned anteriorly and is so drawn. The femur (fe) is considerably thickened and bears several spines on its ventral margin. The mesothoracic leg (Fig. 94) shows no particular modification. The meron (mr_3) of the metathoracic leg (Fig. 95) is elongate and pointed, forming a projecting spinelike structure. The tibia bears several spinelike, movable setae and a row of spines apically. The distal segment of the tarsus (Fig. 96) bears a pair of claws (cl) but no pulvillus.

Lepyronia quadrangularis

Prothorax. The pronotum (prnt, Fig. 67) of the cercopid, *Lepyronia quadrangularis*, is typically saddle-shaped, covering most of the pleuron laterally. Posterodorsally it overlies the anterior part of the mesothoracic tergum, but the pronotum has been displaced anteriorly in figure 66. The epimeron is completely reduced and concealed by the lateral lobe of the pronotum. The sternum (st_1, Fig. 68) forms a trough for the reception of the labium. In other respects it varies but little from the forms already discussed.

Mesothorax. A narrow precosta (pc_1) is demarked anteriorly on the tergum, while the prescutum (psc_2) behind is separated laterally from the scutum (sc_2) by a pair of narrow membranous clefts. The conspicuous scutellum (scl_2) is triangular in shape and its posterior half normally overlies the metathoracic tergum (displaced in Fig. 66). As in the fulgorid the posterior lateral margins of the scutellum are grooved to form a locking device (twg_2) with the bases of the posterior margin of the tegmina.

Laterally, the episternum is divided into an anepisternum (aes_2) and a katepisternum (kes_2). The epimeron (epm_2) and a part of the metathoracic episternum (es_3) is grooved to receive the base of the costal margin of the tegmen. The episternum is broadly united to the sternum. The sternum is differentiated into an anterior prebasisternite (pbs_2), the large basisternite (bst_2), and a furcasternum (fst_2) between the coxal cavities. The furcasternite may possibly be a combination of the furcasternite and the spinasternite found in the orthopteroid orders.

Three axillary sclerites are present dorsally in the basal membrane of the wing, while ventrally there is a well developed subalar sclerite (sa_2) and a considerably reduced basalar sclerite. The mesothoracic spiracle (sp_2, Fig. 67) is located in the membranous region of the pleuron between the pro- and mesothorax.

Metathorax. This segment is well developed and apparently plays an important role in the flight mechanism. In this connection it should be noted that the well developed phragma is an invagination of the anterior margin of the prescutum (psc_3) and is primarily a functional part of the metathorax, in contrast to the cicada in which the well developed phragma is functionally a part of the mesothorax. Further, there is no pronounced development of a postnotum between the mesothoracic and metathoracic terga. The scutum (sc_3) is large and contains a median suture. This median suture (ms_3) is the external demarcation of a well developed median tergal apodeme which unites anteriorly with the phragma. The scutellum (scl_3) forms a narrow posterior margin of the tergum.

Laterally the anterior margin of the tergum gives off two branches. The anterior of these is the postalar bridge (pw_2) of the mesothoracic segment and unites with the mesothoracic epimeron, while the posterior branch forms the prealar bridge (aw_3) of the metathoracic segment and unites with the metathoracic episternum (es_3). The epimeron (epm_3) is united to the postnotum (pnt_3) by a postalar bridge (pw_3). The metathoracic spiracular opening is concealed in the dorsal angle between the mesothoracic postalare and the metathoracic prealare.

The sternum (st_3) is rigidly joined to the mesothoracic furcasternite anteriorly and united with the episternum by a narrow bridge. Although a pair of membranous clefts demark the central region, there is no distinct demarcation of the lateral limits of the sternum.

The basal region of the wing contains three axillary sclerites dorsally, the first axillary sclerite being considerably reduced. Ventrally there is present a subalar sclerite (sa_3) but there is no external evidence of a basalar sclerite. The metathoracic spiracle, although not readily visible, is present in the grooved area formed between the mesothoracic epimeron and the metathoracic episternum in the upper region of the pleuron.

Wings. (Figs. 83 and 84). The fore wing or tegmen is opaque and reticulated, so that some of its venation is obscured. Doering (1922) has been able to delineate the forewing venation by clearing and the venation which she has obtained through this procedure is shown in broken line. A projecting ridge or keel on the underside of the subcosta of the tegmen latches on to a sharp crest of the metathoracic epimeron and helps to lock

the tegmen in place when at repose. The membranous hindwing bears a row of spines or hooks on the costal margin. The basic venation of both fore- and hindwings is indicated in figures 83 and 84.

Legs. The prothoracic (Fig. 97) and mesothoracic legs (Fig. 98) are generally similar, except that the meron (mr_2) of the middle leg is produced into a flat spinelike structure. The hind legs (Fig. 99) are considerably modified. The meron (mr_3) forms a ball-like structure which fits into a socket formed by the epimeron, so that although not united to the epimeron, it is closely associated with it. The tibia (ti_3) has two large spines along its outer edge and a double row of spines at its apex. It is this character of the tibia which is used to distinguish the Cercopidae from the Cicadellidae. The first two tarsal segments also bear an apical row of spines. The last tarsal segment of all the legs bears a pair of claws (cl) and a notched, but single lobed pulvillus (pu), as shown in the tarsus of the mesothoracic leg (Fig. 100). The hind leg of the cercopid bears a considerable resemblance to that of the fulgorid in these respects.

Aulacizes irrorata

Prothorax. The prothoracic tergum takes the shape of a saddle-shaped pronotum as in the previous forms described. It is shown in figure 65 in dotted outline in its normal position covering the mesothoracic tergum. The lateral and ventral aspects (Figs. 64 and 69) of this segment do not vary significantly from that of *Lepyronia quadrangularis* above, except that there is no development of a troughlike structure on the sternum as in the cercopid.

Mesothorax. The mesothoracic precosta (pc_1, Fig. 65) consists of a narrow sclerite, separated from the prescutum (psc_2) by the antecostal. suture (acs_2). The antecostal suture is represented internally by a ridge, not by the development of a phragma. The major portion of the tergum is occupied by the scutum (sc_2). The posterior tergum consists of the scutellum (scl_2), bearing a V-shaped groove (twg_2) for the reception of the basal lip of the posterior margin of the tegmen. The postnotum (pnt_2), completely covered by the scutellar region of the tergum, gives off a postalar arm (pw_2) laterally to the epimeron, whereas the anterior portion of the tergum is united to the episternum by the prealar bridge (aw_2). The membranous base of the wing contains three axillary sclerites dorsally and both a basalar (ba_2) and subalar sclerite (sa_2) ventrally.

The episternum of the pleuron is divided into an anepisternum (aes_2, Fig. 64) and a katepisternum (kes_2). The diagonal line (pwg), dividing the epimeron (epm_3) into two triangular areas, represents a groove into which fits the basal lip of the costal margin of the tegmen, similar to the arrangement found in the cercopid. The mesothoracic spiracle (sp_2) is

located in the upper pleural membranous region between the pro- and mesothorax.

The mesothoracic sternum is also similar to that of the cercopid, there being an anterior prebasisternite (pbs$_2$, Fig. 69), a large basisternite (bst$_2$) and a posterior furcasternite (fst$_2$) between the coxal cavities. The basisternite is divided into two by a median suture, and its posterior margin is demarked by another suture. The furcasternite bears the furcal pits (fp$_2$) which form an internal furcal apodeme. Laterally the sternum is broadly joined with the pleuron.

Metathorax. The mesothoracic postnotum (pnt$_2$, Fig. 65) lies beneath the posterior fold of the mesothoracic scutellum. Morphologically the postnotum is a part of the mesothorax, but as in the cicada it is medially united with the metathorax and laterally with the mesothorax. The large phragma to which the postnotum gives rise through an invagination of its posterior margin is more closely allied with the mesothorax functionally. In this respect it differs from the intersegmental phragma between the meso- and metathoracic segments of the cercopid, which phragma is intimately associated with the metathorax.

The metathorax has no definite prescutal area. The tergum is composed of a large scutum (sc$_3$) and a smaller scutellum (scl$_3$). The metathoracic postnotum (pnt$_3$) behind the scutellum is only sclerotized laterally. A postalar bridge connects the postnotum to the epimeron. Anteriorly, however, there is no distinct prealar bridge to connect the metathoracic tergum to the episternum.

The pleuron consists of a distinct episternum (es$_3$, Fig. 64) and epimeron (epm$_3$) separated by the plural suture (pls$_3$). The metathoracic spiracle (sp$_3$) is located in the membranous region of the pleuron, between the meso- and metathorax. The mesothoracic sternum (bst$_3$, Fig. 69) has a precoxal connection laterally with the episternum. It sends a median process posteriorly between the coxae, where it unites with a postcoxal bridge given off by the epimeron. The trochantin (tn$_3$) of the coxa is quite large and apparently united with the episternum.

Wings. The forewing, or tegmen, is reticulated and thickened. Like the tegmen of the cercopid it is divided by the vannal fold (vf, Fig. 85) into an anterior remigial portion and a smaller posterior vannus. The hindwing (Fig. 86) is membranous, and quite similar, in venation and the presence of a series of hooks on the costal margin, to that of the cercopid. In addition to the vannal fold (vf) it has a jugal fold (jf) which demarks the jugum of the wing. The basic wing venation is indicated in figures 85 and 86.

Legs. The pro- (Fig. 101) and mesothoracic legs (Fig. 102) are comparatively small and similar in appearance. The metathoracic leg (Fig.

103) is several times larger. Its tibia (ti) is square in cross-section, possesses a row of spines along each of four edges, and is fringed with a double row of spines apically. As with the cercopid and fulgorid, the first two tarsal segments are fringed with spines apically. The claws (cl, Fig. 105) borne apically by the third tarsal segment are adherent laterally to the bilobed pulvillus (pu, Fig. 104) in all three legs.

Ceresa bubalus

Prothorax. The membranous cervical region of *Ceresa bubalus* does not contain any cervical sclerites. There are present, however, the paired, triangular, occipital condyles (occ, Fig. 50) borne laterally by the occipital margin of the head.

The unusual development of the pronotum is characteristic of the Membracidae. This structure, important taxonomically, takes on a remarkable variety of shapes throughout the family, developing spines, horns, crests, bulbous structures, and other developments, posteriorly, anteriorly, dorsally and at the humeral angles. Unusual developments of the pronotum are particularly evident in many of the tropical and subtropical forms of this group. According to Funkhauser, the anterior, dorsal, and humeral structures vary haphazardly among the species, and although of almost no value in the differentiation of the higher taxonomic categories, are of considerable value in the delineation of species. The posterior structures, on the other hand, are of a more constant nature and are frequently used for the differentiation of genera.

The cephalic portion of the pronotum, or metopidium (mtp, Fig. 72), of the pronotum, of *Ceresa bubalus* is on a plane continuous with the vertex of the head, and though marked with impunctations, does not possess any special structures. The slightly protruding areas on the lateral margins of the prothorax just above the bases of the forewings are termed the humeral angles (ha), and just above the humeral angles are the lateral projections of the metopidium known as the suprahumeral horns (sh). Obliquely posterior from the suprahumeral horns, a pair of folds meet mesally to form a sharp median edge or carina. The posteriormost portion of the median carina projects as a spinelike posterior process.

The pleural region (Fig. 75) consists of a definite episternal region (es$_1$) bounded laterally by the pleural suture (pls$_1$). A well defined epimeron does not exist, although the lateral lobe of the pronotum just behind the pleural suture may include a portion of the epimeral region. The episternum is turned inwardly immediately behind the head capsule against which it lies. It is joined to the sternum by the precoxa (pcx$_1$).

A posterior view of the prothorax (Fig. 72) reveals a pair of furcal pits (fp$_1$) in the small rectangular sternal plate (st$_1$). The furcal pits

mark the invaginations of the furcal apodemes (fu_1) which possess two branches. One branch runs dorsally, and the other curves laterally and abuts against the pleural apodeme ($plap_1$). The triangular trochantin (tn_1, Fig. 75) lies between the episternum and the coxa.

Mesothorax. This segment is large and well developed. The tergum (Fig. 70) is primarily composed of a large anterior scutum (sc_2) and a posterior scutellum (scl_2). The scutum possesses two pairs of lateral sutures or internal ridges. One pair of such sutures or notaulices (no_2) arises anterolaterally and converges toward the median line, while the second pair runs posteromedially from the anterior notal wing process (anp_2). A narrow precosts or pretergite (pc_1, Fig. 78) is set off from the anterior margin of the scutum by the antecostal suture (acs_2). Posteriorly, the scutellum covers the narrow postnotum (pnt_2) which is united with the metathoracic tergum. The bases of the wings are shown in figure 70, slightly displaced from their normal position at rest. There are three axillary sclerites ($1ax_2$, $2ax_2$, $3ax_2$) in the basal membranous area of the forewing.

The pleuron (Fig. 71) consists of an episternum (es_2) and epimeron (epm_2) separated by the pleural suture (pls_2). The extensions of these sclerites dorsally along the pleural suture form the pleural wing process, or articulation for the wing (pwp_2), while the pleural coxal process, or articulation for the coxa (cxp_2) is formed by the extension of the episternum and epimeron at the ventral extremity of the pleural suture. As in the cercopid and cicadellid previously described, the epimeron possesses a diagonal groove into which the basal costal lip of the fore wing fits when the wings are at rest. A distinct basal region (ba_2) is united to the episternum dorsally, but a corresponding subalar region is not demarked from the upper region of the epimeron. The pleuron is united to the tergum by the prealar bridge (aw_2) joining the episternum to the scutum, and by the postalar bridge (pw_2) joining the epimeron to the postnotum. The mesothoracic spiracle (sp_2, Fig. 71) is in the membranous area just anterior to the prealar bridge.

The sternum (Fig. 74) consists of a central prebasisternite (pbs_2) flanked by the basisternal regions (bst_2). (Compare with the sternum of *Aulacizes irrorata*.) Even if these areas have a homologous value, it is difficult to define their exact limits due to the broad fusion of the sternum with the pleura and the consequent modifications of structure. Detailed comparative studies of intrafamily modifications and relationships are required to clarify the interpretation of these sternal structures. Posterior to the precoxal bridge, a suture demarks a narrow marginal area which Crampton (1915) has designated as the antecoxale (acx_2), similar to such a modification in *Aulacizes irrorata* (acx_2, Fig. 69). Here again it

appears that the median part of this marginal antecoxale is a part of the basisternal region. The furcasternite (fst_2) bearing the furcal pits (fp_2), lies between the coxal cavities. These pits invaginate to form the well developed furcal apodemes (fu_2, Fig. 77), almost reaching to the pleural apodemes ($plap_2$). The remainder of the mesothoracic endoskeleton is formed by a platelike phragma (ph_2, Fig. 76), bearing a deep median notch. The mesothoracic phragma is formed by the invaginated folds between the postnotum and the metathoracic scutum. A narrow post-coxal bridge ($pocx_2$, Fig. 77) units the furcasternite with the epimeron, behind the coxal cavity. The trochantin (tn_2, Fig. 78) is a small sclerite lying in the membranous area between the antecoxale and the coxa.

Metathorax. This segment is considerably smaller than the mesothoracic segment. The major area of the tergum is occupied by the scutum (sc_3, Fig. 70), divided medially by a suture (ms_3). The median suture is represented internally by a median plate which unites anteriorly with the mesothoracic phragma. The narrow posterior margin of the tergum forms the scutellum (scl_3), the lateral extensions of which articulate with the posterior margin of the hind wing by means of the axillary cord (axc_3). Three axillary sclerites ($1ax_3$, $2ax_3$, $3ax_3$) are present in the basal membranous area of the wing adjacent to the anterolateral margin of the scutum.

The pleuron of the metathorax consists of an episternum (es_3, Fig. 71) and epimeron, the latter divided into a large anepimeron ($aepm_3$) and a smaller katepimeron ($kepm_3$). The posterior portion of the mesothoracic epimeron overlies the metathoracic episternum and the metathoracic spiracle (sp_3) is concealed in a small dorsal membranous area between these segments. The pleural wing articulation (pwp_3) and the pleural coxal articulation (cxp_2) are found at the respective dorsal and ventral extremities of the pleural suture (pls_3). A prealar bridge (aw_3), joined to the postalar bridge of the mesothorax, unites the epimeron to the lateral remnant of the postnotum (pnt_3). No distinct basalar or subalar sclerites are present in the articulating membranous area of the wing and pleuron.

The sternum (Fig. 74) is composed of an anterior basisternite (bs_3), and a posterior furcasternite (fst_3) which lie between the coxal cavities. The basisternite is joined to the episternum by a precoxal bridge (pcx_3), while the furcasternite is joined to the katepimeron by a postcoxal bridge ($pocx_3$). The furcasternite bears a median pair of furcal pits which form a small furcal apodeme (fu_3, Fig. 73) internally. The trochantin (tn_3, Fig. 76), closely approximated with the episternum, articulates with the coxa. As seen in this posterior view of the metathorax the lateral rem-

nants of the postnotum, the postalar bridges, the postcoxal bridges, and the sternum, are all united to form a ringlike sclerite around the metathorax.

Wings. Both the fore- (Fig. 87) and hindwings (Fig. 88) are membranous and apparently both pairs of wings are actively used in flight. Funkhauser (1912) has made an excellent comparative study of the wings of the Membracidae, and reference should be made to this study for information concerning the venation. It should, however, be noted that the forewing possesses a vannal fold (vf) along the course of what is probably the second branch of cubitus, which separates the large anterior remigial area from the narrow posterior vannal area, similar to that which occurs in both the cercopid and cicadellid. Funkhauser refers to this vannal fold as the claval suture. The venation* of the wings of *Ceresa bubalus* is noted in figures 87 and 88.

Legs. The prothoracic (Fig. 111) and mesothoracic legs (Fig. 112) are very similar. The coxae, trochanters, femora, tibiae, and three-segmented tarsi of the first two pairs of legs possess no unusual features. The coxae of the jumping metathoracic legs (Fig. 113) are considerably enlarged and their mesal margins each possess an angular, toothed projection which enables the coxae to lock in position against the sternum and each other. The tibia of the hind leg is further modified by the possession of four rows of spines along its length and an apical border of spines. The first tarsal segment is about twice the length of the second tarsal segment, whereas in the pro- and mesothoracic legs the second tarsal segment exceeds the first segment in length. The claws (cl, Fig. 116) adhere to the bilobed, membranous pulvilli (pu) or pads.

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*The interpretation of the wing venation is largely based on the studies of Metcalf (1913a, 1913b, 1917) and Funkhauser (1913). Evans' interpretation (1946a, 1948), in which $R_1 = R_{1a}$, $R_{2+3} = R_{1b}$, and $R_{4+5} = R_2$, may be the more probable one if the position of the cross-vein r is accurately traced.

THE THORACIC MUSCULATURE OF
CERESA BUBALUS

The Cervical Muscles. The movement of the head is controlled by four pairs of muscles (Fig. 50) as follows:

1. A pair of dorsal longitudinal muscles (21) running from the dorsal occipital margin of the head to the lateral pretergal margin of the mesothoracic tergum.

2. A vertical muscle (22) from the dorsolateral occipital margin of the head to the precoxa of the prothorax.

3. A muscle (23) from the occipital condyle to the dorsal, anterior margin of the pronotum.

4. A short, thick muscle (24) from the lateral posterior margin of the hypopharyngeal wing plate to the prothoracic furcal apodeme.

The Prothoracic Muscles. These muscles (Fig. 110) are roughly divided into two groups, one with insertions on the furcal apodeme, the other with insertions on the leg and origins on the pronotum. Besides the muscle going from the furcal apodeme to the hypopharyngeal wing plate, mentioned above, there are two other muscles connected to the furcal apodeme.

1. An anterior muscle (31) from the apex of the furcal apodeme running dorsally to the lower region of the metopidium of the pronotum.

2. A posterior muscle (32) from the apex of the furcal apodeme running dorsally to the lateral margin of the mesothoracic pretergite.

Five prominent muscles, with origins on the lower region of the metopidium of the pronotum are inserted on the trochantin, meron, coxa, and trochanter. Posteriorly these are covered or enclosed by a sclerotized partition (mp) shown in part in figure 72. The muscles (Fig. 110) are as follows:

1. A large muscle (34) originating just beneath the ridge demarking the lower region of the metopidium and inserted on the meron.

2. A muscle (35) originating just below the above one on the metopidium and inserted on the mesal tip of the trochantin.

3. A muscle (36) from the upper lateral corner of the lower region of the metopidium, inserted on the basal rim of the coxa just anterior to the pleural articulation.

4. Similar to the above, but inserted on the basal rim of the coxa, just posterior to the pleural articulation (37).

5. This muscle (38) is inserted mesally on the basal rim of the trochanter. Its origin is near the above two muscles in the lateral corner of the metopidium.

The mesothoracic leg will be used to demonstrate the leg musculature. Since the musculature of the leg segments of the pro-, meso-, and meta-thorax shows a general similarity, further description of the prothoracic leg muscles, not originating on the pronotum, will be omitted at this point.

The Mesothoracic Muscles. An examination of the musculature of this segment at once indicates that of the two wing-bearing segments, the function of flight is chiefly centered in the mesothoracic segment. Previous studies of the flight mechanism of insects have indicated that the flight movements of the wings are performed by two groups of muscles, the indirect wing muscles and the direct wing muscles. The indirect wing muscles, by causing alternating changes in the shape of the thoracic segment, are primarily responsible for the elevation and depression of the wings. These are as follows:

1.   Dorsal longitudinal muscles (41, Fig. 106). A broad pair of median muscles stretched between the mesothoracic phragma and the arched, anterior region of the scutum. These are the chief depressor muscles of the wings.

2.   Oblique dorsal muscle (42, Fig. 107). Laterad of the dorsal longitudinal muscles, this muscle extends from the mesothoracic phragma to the lateral region of the scutum. This muscle acts as a depressor in *Ceresa*, but in other insects, where it becomes nearly vertical in position, it may act as an elevator of the wing.

3.   Tergosternal muscle (43, Fig. 107). This muscle, extending from the anterolateral region of the scutum to the lateral region of the sternum and the precoxal bridge, is the elevator muscle of the wing. (Figures 106, 107, and 108 have been drawn to reveal the muscles as they are dissected from the median line to the lateral wall of the thoracic segments.)

4.   This muscle (47a) extends from the dorsal surface of the projecting pleural apodeme to the anterior region of the posterior notal process.

5.   This short, thick muscle (47b) unites the lateral arm of the furca with the pleural apodeme.

The direct wing muscles act as extensors and flexors of the wing. It is these muscles which are primarily responsible for extending the wings into flight position, and in combination with the natural flexibility of portions of the wing, are responsible for bringing the wings back to rest. Although the function of some of these muscles in this capacity is quite apparent or easy to demonstrate, the exact function of others cannot always be shown, for it is a complex integration of a number of these muscles which is responsible for the various kinds of wing motion. Some

of the indirect wing muscles are inserted upon the coxa and probably play a role in the movement of the leg as well.

1. Basalar muscles. Two muscles are inserted upon the upper portion of the episternum, or basalar sclerite, which invaginates into the body cavity. The first of these (44, Fig. 109) arise from a lateral process of the antecoxal sclerite, while the other (45a) arises from a tendon attached to the basal rim of the coxa just anterior to the pleural articulation. A branch of this latter muscle (45b) goes to the anterior margin of the episternum.

2. Subalar muscle. As has been previously noted there is no distinct subalar sclerite. The muscle which arises from the basal rim of the coxa just posterior to the pleural articulation is the one which usually is inserted on the subalar sclerite in other insects where such a sclerite is present. In this instance the muscle (46, Fig. 112) is inserted upon a small invaginated process on the dorsal margin of the epimeron.

3. Muscle of the 2nd axillary. This muscle (49) arises broadly from the anteroventral margin of the episternum and narrows to a tendon which is inserted upon the 2nd axillary sclerite of the fore wing.

The Ventral Longitudinal Muscles. The ventral longitudinal muscles (50, Fig. 106) of the mesothorax consist of a pair of small muscles extending from the anterior margin of the mesothoracic furca to the posterior faces of the paired sternal apophyses of the prothorax. In addition there is present a pair of short, thick muscles (51) which extend from the raised posterior region of the furca to the lower posterior wall of the phragma.

The Muscles of the Leg. Aside from the muscles mentioned above, which arise on the coxa and are connected with the flight mechanism, there are present a number of leg muscles originating on the thoracic sclerites or their apodemes which are apparently connected with the movements of the leg alone. These muscles are inserted on the coxal and trochanteral segments of the leg and have their origins either on the tergum or on the furcal arms of the sternum. Additional leg muscles are concerned with the movement of the individual leg segments.

COXAL MUSCLES (Fig. 112). ·

1. Tergal promoter of the leg (52, Figs. 107 and 112). This muscle arises on the scutum and is inserted on the ventral end of the trochantin by means of an elongated tendon.

2. Sternal remoter of the leg (53). This muscle arises on the furcal arm of the sternum and is inserted on the posterior basal margin of the coxa.

3. Pleurocoxal muscle (45b). This muscle has already been mentioned in connection with the basalar muscle (45a) of which it is a

branch. Since it arises on the anterior margin of the episternum and is inserted on the basal margin of the coxa just anterior to the pleural articulation, it is in all likelihood directly connected with the movement of the leg.

4. Tergal remoter of the leg (48). This muscle, arising from the posterior corner of the posterior notal process is inserted by means of a tendon on the posterior basal margin of the coxa.

The remaining muscle with a coxal insertion is the subalar muscle (46), inserted on the basal rim of the coxa just behind the pleural articulation.

TROCHANTERAL MUSCLES (Fig. 114).

Two groups of muscles are inserted on the basal margin of the trochanter. The mesal articulation of the trochanter with the coxa bears a long tendon upon which are inserted three muscles. The longest of these muscles (54a) arises on the scutum; the second (54b) originates on the furcal arm, while the third (54c) arises on the wall of the coxa. This group of muscles acts as a depressor of the leg. The second group (55), or extensors of the leg, consisting of several muscle bundles, all arise on the outer wall of the coxa and are inserted on the lateral basal rim of the trochanter.

FEMORAL MUSCLE (56, Fig. 114).

A single small muscle, inserted on the basal rim of the femoral segment, has its origin on the wall of the distal portion of the trochanter.

TIBIAL MUSCLES (Fig. 115).

1. Extensor muscle. This muscle is inserted on the outer basal margin of the tibia by means of a tendon. The tendon bears two groups of muscles, one originating on the wall of the distal portion of the trochanter (57a), the other originating on the wall of the femur (57b).

2. Depressor muscles (58). A pair of short muscles inserted on opposite sides of the inner basal margin of the tibia, arising on the distal portion of the femur.

TARSAL MUSCLES (59, 60, Fig. 116).

These consist of two short bundles inserted on opposite sides of the basal rim of the proximal segment of the tarsus, arising on the wall of the distal end of the tibia.

POSTTARSAL MUSCLE (61a, Fig. 116).

The unguitractor (unp) of the posttarsus continues into the tarsus and tibia in the form of a long unguitractoral tendon (unt) upon which are inserted two muscle branches, one arising on the wall of the middle portion of the tibia (61a), the other arising on the wall of the proximal portion of the tibia (not shown).

The Metathoracic Muscles. The muscles of the metathorax bear very little resemblance to those of the mesothoracic segment. The most striking feature is the complete absence of those muscles termed the indirect wing muscles, the dorsal longitudinals, the oblique dorsals and the tergosternal muscles. The absence of these muscles precludes the possibility that the flight mechanism of the hind wings is in any way similar to that of the fore wings.

The most conspicuous muscles are those associated with the legs. The leg, wing, and other muscles of the metathorax are listed as they are seen in a median section of the thorax and dissected away toward the lateral wall, as follows:

1. Trochanteral extensor of the leg (62a, Fig. 106). This is a large, conspicuous muscle with a tendonal insertion upon the mesal, basal margin of the trochanter, and originating partly on the posterior wall of the mesothoracic phragma and partly on the scutum. A branch of this muscle (62b) inserted upon the same tendon extends to the posterior face of the mesothoracic furca. Another branch (not shown) originates on the wall of the coxa.

2. Adductor of the coxa (63). A small muscle arising on the posterior of the metasternal furca and extending, posteriorly and ventrally, to the inner, posterior margin of the base of the coxa.

3. Ventral muscle (64). This is a short muscle extending from the posterior surface of the metasternal furca to the postcoxal bridge.

4. Tergal remoter of the coxa (65, Fig. 107). A muscle arising on the anterolateral corner of the scutum, inserted by means of a tendon on the lateral rim of the base of the coxa just behind the pleural articulation.

5. A broad, flat muscle (66) inserted on the anterior rim of the base of the coxa; origin on the anterior margin of the episternum.

6. A muscle (67) extending from the trochantin, attached by a tendon to the anterolateral corner of the scutum.

7. A muscle (68) extending from the precoxal bridge to the anterolateral corner of the scutum.

8. A short, narrow muscle (69, Fig. 108) extending from the pleural apodeme to the anterior notal wing process.

The following muscles have their insertion upon the axillary sclerites of the wing.

1. A muscle (70) extending from the lateral shelf of the base of the coxa just behind the pleural articulation to a tendon inserted on the second axillary sclerite.

2. A muscle (71, Fig. 117) extending from the rim of the base of the coxa just behind the pleural articulation to the posterior lever of the third axillary sclerite.

3. A muscle (72) arising on the ventral margin of the anepimeron and inserted on the anterior lever of the third axillary.

ABDOMINAL SEGMENTS OF AUCHENORHYNCHA

The abdomen of auchenorhynchous Homoptera consists of eleven distinct segments, and the first eight abdominal segments bear spiracular openings. In the past, the proper enumeration of the abdominal segments has sometimes caused confusion, due in large part to the modifications of structure of the two basal segments which form the articulation between the thorax and the remainder of the abdomen. A reduced sclerotization of the terga and sterna of these two segments, and the development of extensive intrasegmental areas of membranization have been largely responsible for the difficulty of delineating the true segmental limits. The picture has been further complicated by the fact that the metathoracic postnotum, usually separated from the thorax by a well defined membranous area in other paurometabolous insects, frequently forms a complete ring with the metathoracic postcoxal bridges which is firmly united with the thorax.

The true segmental limits of the abdomen are marked internally by the intersegmental ridges upon which the dorsal and ventral longitudinal muscles are attached. Externally these intersegmental ridges may be marked by lines or sutures, termed the antecostal sutures, which indicate the primary segmentation. The flexibility of the primary segments has been brought about by a comparatively narrow intrasegmental membranization of the posterior portion of the primary segment, which has resulted in a functional or secondary segmentation. Normally the primary segment between two antecostal sutures, or intersegmental ridges, consists of a wide, anteriorly-sclerotized plate followed by a comparatively narrow, posterior membrane, which is in turn followed by a very narrow rim of sclerite, sometimes absent, just before the succeeding intersegmental ridge. It will be seen that in the basal segment of the representatives of the Auchenorhyncha under discussion, the primary segment sometimes consists of a narrow anterior rim of sclerite, followed by a wide intrasegmental membrane, and a narrow or wide posterior sclerite. Other modifications of the first and second segments will be discussed in the descriptions of structure which follow. In general, it may be pointed out that where the enumeration of abdominal segments presents difficulty, it is possible to get one's bearings by locating the eighth abdominal segment which bears the last pair of abdominal spiracles.

Scolops pungens

Visceral Abdominal Segments. The partially distended abdomen of a female is shown in lateral view in figure 119. The postnotum (pnt$_3$) is a

broad sclerite stretching across the dorsum, broadly united to the epi-
meral regions (epm$_3$) on each side. The first tergite (It) consists of a
narrow anterior margin of sclerite firmly united with the postnotum, and
a larger, bilobed posterior sclerite. These sclerotized regions are separated
by a narrow membranous area. The bilobed areas on either side are
united dorsomesally by a narrow sclerite, while the anterior of the bilobed
sclerites unites with the anterior rim of the first tergite, which is in turn
united to the postnotum. The first spiracle (sp$_1$) is located in the mem-
branous tergal region just behind the posterolateral corner of the post-
notum. The second tergum (IIt) consists of a broad, anterior sclerite
separated from a smaller posterior sclerite by a membranous region. Lat-
erally, a small arm of sclerite unites the anterior and posterior tergites of
the second tergum. The second spiracle (sp$_2$) is located in the antero-
lateral membrane of the second tergum. The narrow posterior sclerotized
portion of the second tergum is firmly joined to the broad sclerotized
region of the third tergum. The terga of segments three to eight are
uniform, each consisting of a broad, anterior sclerite, and a posterior
membrane. The spiracles of these segments are located in the mem-
branous area between the lateral margins of the median tergites and the
laterotergites (ltg).

The lateral sclerotized regions below the spiracles are regarded as
laterotergites in view of the fact that in other fulgorids the spiracles are
located in the upper halves of these sclerites. According to the studies
of Snodgrass, the dorsopleural line, which demarks the lower limits of the
dorsum, or tergal region, is always formed below the spiracles. Since the
spiracles do occur in these lateral sclerites in other fulgorids, it would
appear that these sclerites belong to the terga, and are consequently
here termed laterotergites.

Ventrally the first sternal segment (Is, Fig. 118) consists of a narrow
anterior semicircular sclerite which appears to arise from the region
where the posterolateral corner of the postnotum meets the epimeron,
and a narrow, median, posterior sclerite, separated by a membranous
region. The second sternal segment (IIs) likewise consists of narrow
anterior and posterior sclerites separated by a membranous region. Lat-
erally this posterior sclerite of the second sternal segment broadens and
fuses with the laterotergite. Sternal segments three to seven consist of
broad, anterior sternal plates, each followed by a membranous region.
It should be mentioned that these definitive sternal plates are evidently
composite plates, formed by the union of the primary sterna with the
lateral pleural regions. Morphologically then, these definitive sternal
plates are coxosterna or pleurosterna.

The Female Genitalia and Terminal Abdominal Segments. Examina-

tion of the structural parts of the ovipositor of *Scolops pungens* will indicate that the fulgorids have retained an exceedingly primitive form of this organ. The eighth tergum (VIIIt, Fig. 131), although reduced in size, possesses the normal structure of the preceding terga. The definitive eighth sternal plate, however, has become modified. It consists of two lateral halves (1vlf, Fig. 132) separated medially by a membranous area. These give rise at their posteromesal angles to the arms or first valvulae (1vl) of the ovipositor. It can be seen that the separate halves of the definitive eighth sternal plate represent the highly modified first valvifers of the more specialized ovipositors of other families of Auchenorhyncha.

The ninth tergal plate (IXt) gives rise at its lateral margin to a pair of elongated sclerites which extend ventrally. The anterior of these lateral branches of the ninth tergum bends posteriorly and unites with the dorsal edge of the sclerotized portion of the first valvula. As will be seen later this lateral branch of the ninth tergum represents the origin of the inner ramus (1ri) of the first valvula. The posterior, lateral branch of the ninth tergum (2vlf) gives rise ventrally to the second valvula (2vl) and to the broad bilobed flaps dorsally which form the third valvula (3vl). It would appear that this posterior lateral arm of the ninth tergum represents the second valvifer of the specialized homopteran ovipositor.

The nature of the terminal abdominal segments in the fulgorids is distinct from that found in the cicadas, cercopids, cicadellids, and membracids. Posteriorly, the ninth tergum forms a narrow ring which runs ventrally beneath the tenth segment. The tenth segment (X) forms a broad flaplike plate which extends over the dorsal margins of the third valvulae. Its dorsal surface contains a hollowed area in which the circular eleventh segment (XI) rests. The eleventh segment bears a single posterior projection which is termed the anal style (as). It has been suggested that the anal style may represent the fused cerci of orthopteroid insects. The anus opens caudally on the eleventh segment between the base of the anal style and the overhanging posterior margin of the eleventh segment.

The Male Genitalia and Terminal Abdominal Segments. The ninth segment (IX, Fig. 133) of the male consists of a single sclerotized plate which forms a complete ring around the abdomen. Protruding caudoventrally from the membranous area behind the sclerotic ring of the ninth segment is a pair of large, blunt parameres (pm), each with a hooked projection on the dorsal margin. Above the parameres is the aedeagus (aed). It consists of a basal ring of sclerite from which a pair of lateral, apically bifurcating, arms are given off posteriorly. Above and below these lateral arms, the aedeagus is membranous. The opening of the

aedeagus, or gonopore (gnp), lies in the membranous lobe above. Be-
tween the base of the aedeagus and the base of the parameres, there is
present a median, inverted Y-shaped sclerite, or basal plate (not shown).
The stem of the Y forms an elongate process which extends to the base
of the aedeagus, and each short arm of the Y-shaped basal plate articu-
lates with the base of a paramere. It should be noted that the bases of
the parameres do not possess apodemal processes which extend into the
body cavity as occur in the cercopid, cicadellid, and membracid. Above
the aedeagus is the flaplike tenth segment (X). Both the tenth and
eleventh (XI) segments are generally similar to the corresponding seg-
ments of the female.

An excellent, comprehensive study of the comparative structure of the
male genitalia of Rhynchota, including the Auchenorhyncha, has been
made by Singh-Pruthi (1924).

Tibicina septendecim

Visceral Abdominal Segments. The general structure of the abdomen
of the cicada has been adequately covered by other writers, but is in-
cluded here, for its comparative value, with the other representatives of
the Auchenorhyncha which are discussed. The female abdomen of *Tibi-
cina septendecim* is shown in lateral view in figure 121. The postnotum
(pnt₃) is a narrow sclerite extending to the epimera on each side. The first
abdominal tergum (It) consists of two sclerotized portions separated by
a membranous area. A narrow, anterior sclerotized margin of the first
tergum is united to the posterior margin of the postnotum, while the
wider posterior sclerite is joined to the anterior edge of the second ter-
gum. These sclerotized portions of the first tergum are joined laterally.
The first abdominal spiracle (sp₁) lies in the anterolateral corner of the
first tergum immediately behind the postnotum.

Tergal segments two to eight consist of broad, arched plates of sclerite
anteriorly, followed by posterior segmental membranes. The eighth tergal
segment is wider than the terga of the preceding visceral segments.

The first abdominal sternum (Is, Fig. 120) consists of a median, pen-
tagonal plate fused with the posterior margins of the metathoracic post-
coxal bridges (pocx₃). It is divided into two parts, the posterior of
which folds into the tympanal cavity. The second sternum (IIs) also con-
sists of two parts. An anterior, median rectangular plate, united with
the posterior margin of the first sternal plate, likewise folds into the
tympanal cavity and sends out a pair of narrow arms laterally. The sec-
ond pair of abdominal spiracles (sp₂) is located in the lateral expansions
of the distals ends of these arms. Between these lateral arms of the anterior
half of the second sternum and the anterior margin of the posterior half

lie the tympana (typ) or so-called "mirrors," of the auditory organ. The auditory capsule (au) which contains an innervated sense organ, or chordotonal organ, is a tubercle-like, rounded swelling with a slit-shaped membrane on the ventrolateral portion of the second abdominal tergite.

The first two abdominal segments of the male are generally similar in structure to those of the female, except for those modifications of structure associated with the presence of the sound-producing organs peculiar to the male. The ventrolateral portions of the first abdominal tergum are modified to form the large, oval membranous areas, or tymbals (tyb, Fig. 58), which bear conspicuous, parallel, riblike markings.

It has been previously mentioned that the metathoracic epimera of the male are produced posteriorly to form the opercula (opc, Fig. 61) which cover the tympanal chambers. The posterior half of the first abdominal sternum is longer, and the membranous area between the lateral arms of the first and second sterna is larger, than the corresponding parts in the female, so that the tympanal cavity of the male is of greater dimensions than that of the female. The V-shaped lateral arms of the anterior portion of the second sternum are wider and stronger than the homologous arms of the female. It should be noted that Myers (1928), in his comparative studies of the Cicadidae, has followed the error of Vogel in considering these arms as "differentiated anterior parts of the first sternite" and the tympana as "differentiated posterior parts of the first sternite." The correct homologies have been pointed out by Snodgrass (1933).

The song of the male is produced by the contractions of the powerful V-shaped tymbal muscles which extend from either side of the median, keeled, endoskeletal structure of the anterior portion of the second sternum to a pair of internal, sclerotized plates just beneath the tymbal membranes. A short tendon extends from the center of each sclerotized plate to the posteromesal sclerotized corner of each tymbal. According to Myers the contraction and release of the tymbal muscles causes the tymbal to produce a clicking sound. It is an extremely rapid series of such clicks, said to be amplified by the large abdominal air sacs which open directly to the exterior through the first abdominal spiracles, that produces the "song" of the cicada. As in the female, there is an auditory capsule present in the ventral portion of the second abdominal tergum. In the female (Fig. 121), it may be seen that the sterna of segments three to six consist of broad, anterior definitive sternal plates, each of which is followed by a narrowed membranous area. Laterally the sternal plates are united with the tergal plate, each forming a complete ring around the abdomen. The spiracles of these segments are located in the anterolateral corners of the sterna, just beneath the lateral margin of the

tergal plates. The sternal plate of the seventh segment is deeply and broadly notched along its posterior margin.

Following a preliminary discussion of the nature and composition of the abdominal segments of insects, Myers (1928) concludes that each of the abdominal segments in a cicada consists of "a strongly over-arched tergite meeting an entirely ventral sternite, which bears the spiracles," and apparently considers that the pleural areas are not included in the definitive sternal plate. As has been noted, the first valvulae of the fulgorid ovipositor arise from the first valvifers, or limb base of the eighth segment, which are homologous with the lateral portions of the definitive sternal plates of the preceding segments. There is no question here that the pleural regions are incorporated into the definitive sternal plates of the fulgorid. Unless it can be shown that the cicadas represent a special group among the Auchenorhyncha in which the definitive elements of the abdominal segments differ from those of the other families, there would seem little reason to consider that the segmental elements of the cicadas consist only of tergal and sternal portions.

The Female Genitalia and Terminal Abdominal Segments. The terminal abdominal segments of the cicada are shown in lateral view in figure 134, with the sclerites somewhat displaced to show their relationship. The eighth tergal plate (VIIIt) is generally similar to the preceding tergal plates, except for the fact that it abruptly tapers at its lateroventral margin. In the membranous region beneath the lateroventral margin of the eighth tergal plate lies the eighth abdominal spiracle. Below this is the first valvifer (1vlf), which gives rise at its anteroventral margin to the first, or ventral valvula (1vl) of the ovipositor. Two rami, or sclerotic rods, which run along the ventral and dorsal margins of the first valvula strengthen it, and the dorsal or inner ramus forms a track along which the second or inner valvula (2vl) of the ovipositor moves. The dorsal or inner ramus of the first valvula is given off by the small plate (rp) between the first valvifer and the anteroventral angle of the ninth tergite, which plate is united with the ninth tergal plate. The first valvula is thus united with the ninth tergal plate by means of the inner ramus and ramal plate.

The second valvifer (2vlf) is also joined with the ninth tergal plate. The union, of the ramal plate and the second valvifer, with the ninth tergal plate, is a condition apparently homologous with the union of the corresponding parts of the fulgorid ovipositor with the anterior and posterior lateroventral arms of the ninth tergal plate.

The second or middle valvulae (2vl) are borne by the anterior margins of the second valvifers, while the posterior margins give rise to the third or dorsal pair of valvulae (3vl). The second valvulae, united along

their dorsal edges and grooved ventrally, fit within the first valvulae, and together provide a passage for the eggs. The third valvulae are a pair of flaplike structures into which the terminal portions of the ovipositor are withdrawn when at rest. Snodgrass has pointed out that the genital chamber of the female has two openings, an anterior large opening (gnp, Fig. 134) in the membranous vestibulum behind the seventh sternal plate, and a smaller posterior opening between the bases of the second valvulae (not shown).

The terminal abdominal segments consist of a short annular tenth segment (X, Fig. 137) which bears a ring of sclerite, widening ventrally, and the smaller eleventh segment (XI).

The Male Genitalia and Terminal Abdominal Segments. The eighth tergal plate of the male (VIIIt, Fig. 136) has no special modification. The eighth sternal plate (VIIIs), however, is a shovel-like structure extending considerably posterior of the eighth tergal plate. Between these plates lies the eighth spiracle (sp_8). The ninth segment (IX) is represented by a circular ring of sclerite sometimes termed the pygophor, or pygofer. The ninth segment and aedeagus (aed) are shown in caudoventral view in figure 138. The pygophor is seen to be broadly ringed dorsally and narrowed ventrally, with toothed, caudoventral margins. The aedeagus is an elongate, sclerotized tube arising in the caudal membranous region of the pygophor. A basal plate (bp), bearing a pair of divergent arms, is united with the base of the aedeagus. The genital opening or gonopore (gnp) is located apically in the expanded membranous region of the aedeagus. A pair of hooklike sclerotized structures are present in this membranous area, one on either side of the gonopore.

The aedeagus is kept in place by the paired ventral claspers (vc) of the tenth segment. The tenth and eleventh segments are shown laterally in figure 130. The ventral claspers are large, hooked sclerotized appendages, firmly united with the sclerotized ring of the tenth segment. The eleventh segment (XI) is circled by a narrow band of sclerite and bears the anal style (as). If the anal style represents the cercus of the eleventh segment, the small oval sclerotized plate at its base may be the base of the cercus, or basicercus. It should be noted that in the male genitalia of the cicada, both the parameres and subgenital plates are absent, although parameres are present in the primitive cicada *Tettigarcta tomentosa.*

Lepyronia quadrangularis

Visceral Abdominal Segments. The sclerotized portion of the first abdominal tergum (It, Fig. 123) of the female cercopid, *Lepyronia quadrangularis,* is mainly confined to the lateral area, in which a small anterior plate united with the posterior margin of the postnotum is bridged with

a large posterior plate. The posterior plates of the first tergum on each side are united by a narrow rim of sclerite across the mid-dorsal line. The small, first abdominal spiracular opening (sp$_1$) located in the membranous area immediately behind the metathoracic postnotum is inconspicuous and sometimes difficult to locate.

The anterolateral margin of the second abdominal tergal plate (IIt) is united to the first tergal plate, and its posterior border is firmly joined to the third tergal plate, so that no segmental movement is possible between the second and third terga. The second abdominal spiracle (sp$_2$) is located at the anterolateral corner of the second tergal plate. The third tergal segment (IIIt) consists of a sclerotized, broad, anterior plate and a posterior membrane. The third spiracle is located in the anterolateral corner of the definitive sternal plate. In segments four to six there is a partial membranization of the tergal plate laterally to form laterotergites (ltg). The seventh and eighth tergal segments are of normal structure. The fourth to eighth abdominal spiracles are located in membranous folds between their tergal and sternal plates.

The first abdominal sternum (Is, Fig. 122), consisting of a sclerotized, anterior, median plate and a posterior, narrow fringe of sclerite, is located between the postcoxal bridges (pocx$_3$) and posterior intersegmental line (is). The lateral areas are membranous. The second abdominal sternum (IIs) consists of a narrow anterior rim of sclerite which borders the intersegmental line, joined by two lateral arms to a wider, posterior sclerite. The definitive sternal plate of the third segment (IIIs) has a median tubercle-like projection on its posterior margin. Sternal segments four to seven are similar in structure, each consisting of a wide, anterior plate of sclerite followed by a posterior, segmental membrane.

The Female Genitalia and Terminal Abdominal Segments. The structural elements of the female genitalia of the cercopid, *Lepyronia quadrangularis,* are similar to those of the cicada. In figure 139, the parts of the ovipositor are shown in almost their normal resting position. In figure 128, these parts have been considerably displaced to show their relationship. The first valvifers (1vlf) give rise ventrally to the paired, first valvulae (1vl). The second valvifers (2vlf), joined to the ninth segment (IX), give rise anteriorly to the second valvulae (2vl), the basal halves of which are united dorsally, and posteriorly to the flaplike third valvulae (2vl). The second valvulae move along a sclerotized track on the inner faces of the first valvulae formed by the inner ramal arms (lri), of the first valvulae. The inner ramal arm of each first valvula is joined to the ramal plate (rp) which is in turn united with the anterior margin of the sclerotized plate of the ninth tergite (IXt).

The terminal abdominal segments (Fig. 139) of the cercopid are

short. The tenth segment (X) is evidenced by a narrow ring of sclerite. The eleventh segment (XI), in addition to a complete anterior ring of sclerite bears a saddle-shaped sclerite, and a pair of small plates at the base of the anal styles. The anus (an) lies between the bases of the anal styles (as). Ventrally, between the paired anal styles, there is present a median sclerite. All of these sclerotized portions of the terminal segments of *Lepyronia quadrangularis,* unlike the corresponding parts of some of the other Auchenorhyncha, are well sclerotized and distinct.

The Male Genitalia and Terminal Abdominal Segments. The ninth segment (IX, Fig. 140) of the male consists of a complete ring of sclerite to which the ventral subgenital plates (gp) are united. A small posterior sclerite is separated dorsally from the main ring of the ninth segment. Protruding caudally from the membrane above the subgenital plates are the paired parameres, the basal plate and the aedeagus. The relationship of these parts is shown in figure 129. The parameres (pm) are paired structures, on either side of the basal plate (bp), each bearing several hooklike spines or projections. The basal plate is triangular in shape and bears a membranous area apically from which the base of the aedeagus originates. The aedeagus bears a pair of bifurcating processes apically, between the bases of which is the genital opening or gonopore. A slender median membranous process lies between the two sclerotized bifurcating processes.

The ringed, sclerotic plate of the tenth segment (X, Fig. 140) is larger than that of the female, but in other respects the terminal abdominal segments of the male are similar to those of the female.

Aulacizes irrorata

Visceral Abdominal Segments. The visceral segments of the abdomen of the cicadellid *Aulacizes irrorata,* except for the two basal segments, are subcylindrical and of an almost uniform width and breadth. The first tergum (It, Fig. 125) consists of an anterior sclerotized region united with the postnotum (pnt₃) and a posterior sclerotized region united laterally with the anterior plate by an oblique bridge of sclerite. The first spiracle (sp₁) lies in the membranous region of the anterolateral corner of the first tergal segment just behind the postnotum. The second tergum (IIt) consists of an anterior sclerotized region and a narrow posterior rim of sclerite separated by a membranous area. The true limits of the first and second tergal segments are marked by the intersegmental lines (is). The second spiracle (sp₂) is located in the membranous region immediately below the anterolateral corner of the broad anterior sclerite of the second tergum. The terga of segments three to eight are generally uniform in structure, each consisting of a wide, anterior sclerotized plate

and a narrow, posterior segmental membrane. Each tergal plate of these segments is differentiated into a laterotergite (ltg) bearing a spiracle in its anterolateral corner. The laterotergite of the third segment is somewhat enlarged and articulates with the posterior margin of the metathoracic epimeron.

The basal sternal segments are shown in figure 124. The first sternal segment (Is) consists of a median sclerotized area, between the metathoracic postcoxal bridges (poxc₃) and the anterior bar of sclerite of the second sternal segment, and lateral membranous areas. The anterior bar of the second sternal segment (IIs) is followed by a membranous area and a broad W-shaped sclerite. The anterior and posterior regions of sclerite of the second sternum are united laterally. The third to sixth segments consist of anterior, broad, rectangular plates of sclerite followed by membranes. The seventh segmental plate of the female abdomen, which covers the valvifers and bases of the valvulae of the ovipositor, has a convex posterior margin.

The Female Genitalia and Terminal Abdominal Segments. The first valvifers (1vlf, Fig. 141) bear the flat, first valvulae (1vl) of the ovipositor. On the ventral edge of the first valvula is a thickened rod of sclerite, the outer ramus (1ro). The inner ramal arm (1ri) which connects with the ramal plate (rp) runs along the middle of the inner face of the first valvula and gradually disappears toward the apex. The ramal plate is broadly united with the anterolateral region of the tergal plate of the ninth segment (IXt).

The second valvifers (2vlf) bear the second, or middle valvulae (2vl) from their anterior regions and the third or dorsal valvulae (3vl) from their posterior regions. The second valvulae are membranous basally, flatly compressed, have strong saw-toothed dorsal margins apically, and are separate. An outer ramus (2ro) runs along the ventral edge of each second valvula. The dorsal half of the inner face of each first valvula is closely appressed to the ventral half of the outer surface of each second valvula, and it may be possible that the first and second pairs of valvulae act in unison as one pair of appendages. In their resting position they are sheathed by the third valvulae.

The tenth segment (X) is a short, ringed segment, only partially sclerotized ventrally. The eleventh segment (XI) bears an anterior ring of sclerite, two small sclerites on each side and the apical, paired anal styles (as) which are united along their median edges by a membrane.

The Male Genitalia and Terminal Abdominal Segments. The ninth segment (IX, Fig. 142) of the male is completely ringed by sclerite. Posteroventrally the paired subgenital plates are united with the ninth annular sclerite. Exserted from the caudoventral membranous region of

the ninth segment are a pair of short, bluntly rounded parameres (pm). Lying medially between the parameres and extending to the base of the aedeagus (aed) is the single, elongate, basal plate (bp). Proximally this basal plate bears a pair of diverging arms, and in this species, it can be seen that the arms of the basal plates articulate with the inner, basal parts of the parameres. The aedeagus bears a pair of diverging sclerotized, sharply pointed arms dorsally. Anterior to these arms and arising at their base is a median projection, sclerotized anteriorly and laterally, but membranous posteriorly, which bears the opening, or gonopore (gnp), of the aedeagus apically. Between the aedeagus and dorsoposterior margin of the ninth annular sclerite on each side, and apparently differentiated from it, is a pair of knoblike sclerotized plates. The tenth abdominal segment (X) is almost entirely reduced to membrane, while the parts of the eleventh segment are essentially identical to those of the female.

Ceresa bubalus

Visceral Abdominal Segments. The abdomen of the female membracid, *Ceresa bubalus*, shown in lateral view in figure 127, is highly arched, somewhat compressed laterally, tapers posteriorly, and is suggestive of the structure and shape of the abdomen of the cicada, *Tibicina septendecim.* The first tergum consists of an anterior rim of sclerite united with the metathoracic postnotum (pnt$_3$), and a posterior sclerite united with the anterior margin of the tergal plate of the second segment (IIt). These sclerotized regions of the first abdominal tergum are joined by an oblique bridge of sclerite laterally. The intervening areas are membranous. The first abdominal spiracle (sp$_1$) is located laterally in the anterior rim of sclerite immediately behind the metathoracic postnotum.

The second tergal segment (IIt) consists of a single plate of sclerite, the anterior half of which rises abruptly upward to meet the posterior half of the plate. The latter half is bent at approximately right angles to the anterior portion. The posterior margin of the second tergal plate is rigidly united to the third tergal plate, there being no intervening segmental membrane. The second abdominal spiracle (sp$_2$) lies in the membrane below the anterolateral region of the second tergal plate.

The third to seventh abdominal terga, except for a successive reduction in width, are uniform, each consisting of a highly arched anterior plate of sclerite followed by the posterior segmental membrane. The eighth tergum is wider than the preceding segment, and tapers anteroventrally. A ventrolateral region of each of tergal plates three to eight bends underneath the abdomen, in a plane with the sternal plates, to form the laterotergites (ltg). The spiracle of the third segment is located in the anterodorsal corner of the laterotergite, while the spiracles of the

succeeding four segments are each located in the anteroventral corner of their corresponding laterotergites. The eighth abdominal spiracle is located dorsocentrally in the eighth laterotergite.

The first sternal segment (Is, Fig. 126) consists of lateral membranous areas and a median, trapezoid-shaped plate of sclerite. The smaller anterior margin, and the wider posterior margin of this median plate respectively are united with the metathorax and the second sternal plate. The second sternal segment (IIs) consists of anterior and posterior plates of sclerite separated by a middle region of membrane. The posterior plate of the second sternum is united with the sternal plate of the third segment (IIIs). Each of segments three to six consists of an anterior rectangular plate of sclerite separated by membranous regions from its own laterotergites and the succeeding segment. The seventh definitive sternal plate is longer than those of the preceding segments and its posterior margin is notched medially.

The Female Genitalia and Terminal Abdominal Segments. A lateral view of the genital segments and the parts of the ovipositor is shown in figure 149. The seventh sternal plate partly covers the paired first valvifers (1vlf). The first valvifer gives rise to an outer, ventral blade, or first valvula (1vl) of the ovipositor. The anterior regions of the second valvifers (2vlf) bear the inner middle blades, or second valvulae (2vl) of the ovipositor. The second valvulae are united dorsally, forming a ventral groove for the passage of the eggs, and have a dorsal, saw-toothed edge apically. The flaplike dorsal, or third valvulae (3vl), which sheath the blades of the ovipositor, arise from the posterior region of the second valvifers. The relationship of the second and third valvulae to the second valvifer is shown in figure 147.

Each ventral blade of the ovipositor possesses both an outer and inner ramus, while the middle blade possesses only an outer ramus. The relationship of these rami, the other parts of the ovipositor and the ninth tergite are best seen in internal view shown in figure 148. The outer rami (1ro) run along the ventral margin of the first valvulae and form a track by means of which the first valvulae slide upon one another. The inner ramus (1ri) which runs along the dorsal edge of the first valvula arises from the ramal plate (rp) which is united with the anterolateral corner of the ninth tergite (IXt). The outer ramus (2ro) of the second valvula runs along the ventral edge of the latter, and together with the inner ramus of the first valvula forms a track, one on each side, by means of which the inner valvulae slide on the outer valvulae. The second valvifer is connected by a short thick bar of sclerite to the inner margin of the anterolateral corner of the ninth tergite.

In the ventral view of the genitalia shown in figure 144 the seventh sternal plate has been pulled back to expose the valvifers and the bases of the valvulae. The genital opening, or gonopore (gnp) by means of which the eggs pass from the median oviduct to the ovipositor, is shown between, and at the base of, the second valvulae.

The terminal abdominal segments are shown in figure 145. These segments in the female present a rather unusual arrangement. The posterior margins of the ninth tergal plate are bounded by an annular membranous region which invaginates within the ninth segment and gives rise to a sclerotized cylindrical tube which is apparently a part of the tenth abdominal segment (X). Within this outer portion of the tenth segment is another tube, somewhat less strongly chitinized, but its anterior margin is rigidly united with the anterior margin of the outer, tubelike portion. This inner, tubelike segment is apparently a posterior portion of the tenth segment. The posterior portion of the tenth segment is followed by a membranous section, followed in turn by another annular sclerite which is a part of the eleventh segment (XI). The remainder of the eleventh segment consists of the anal styles (as) and small paired, basal sclerites.

The Male Genitalia and Terminal Abdominal Segments. The male genitalia are shown in lateral view in figure 151. The ninth tergum (IXt) consists of a saddle-shaped tergal plate, broad dorsally and narrowing laterally. On each side the caudoventral region of the ninth tergal plate is differentiated into a flaplike plate bearing an immovable spine (ts). Ventrally, the ninth segment forms a single subgenital plate (gp), which is notched posteriorly. It is shown in ventral view in figure 154. The subgenital plates of other species of membracids, belonging to the genera *Aconophora, Platicotis, Campylenchia, Enchenopa,* and others, consist of either entirely separate paired genital valves and a separate sternal plate, or show these parts in varying degrees of fusion. It therefore appears that the subgenital plate of *Ceresa bubalus* consists of the fused genital valves and ninth sternal plate.

Above the subgenital plate are the elongate, paired parameres (pm). Between the bases of the parameres and extending to the base of the aedeagus is the median basal plate (bp). The aedeagus (aed) is a median, hollow, rodlike structure with an elongate, vertical membranous region caudally which bears the slit-shaped gonopore (gnp). The aedeagus is shown in figure 155, in caudal view. There is a median sclerotized plate, apparently a part of the basal region of the aedeagus, extending to the anteroventral margin of the tenth segment.

The terminal abdominal segments of the male differ from those of the female. The tenth segment (X, Fig. 151) bears none of the modifications of the female, but consists of an annular sclerite followed by a membranous region. The eleventh segment (XI) also has an anterior annular sclerite and paired anal styles (as). The relationship of the terminal abdominal segments and genitalia is shown in caudal view in figure 150.

THE ABDOMINAL MUSCULATURE OF
CERESA BUBALUS

Muscles of the Visceral Abdominal Segments. The muscles of the abdominal segments of *Ceresa bubalus* are shown in figure 143 and may be classed in three general groups. These are the dorsal longitudinal muscles, the ventral longitudinal muscles, and the lateral muscles. The dorsal longitudinal muscles are in some segments subdivided as median dorsal longitudinal muscles and lateral dorsal longitudinal muscles. These are as follows:

DORSAL LONGITUDINAL MUSCLES (d).

These muscles extend between the intersegmental ridges, or antecostae, of successive terga, the intersegmental ridges being present on the anterior margins of the tergal plates. In the middle, visceral abdominal segments these muscles are separated into two groups, the median dorsal longitudinal muscles (dm) found on either side of the mid-dorsal line of the terga, and the lateral dorsal longitudinal muscles (dl) extending across the lateroventral portions of ventral longitudinal muscles (v).

VENTRAL LONGITUDINAL MUSCLES (v).

These muscles extend from the intersegmental ridges, or antecostae, of the successive sterna, the intersegmental ridges being present on the anterior margins of the definitive sternal plates. The muscles are located in the lateral regions of the sternal plates.

LATERAL MUSCLES (l).

These muscles extend from the lateral margins of the definitive sternal plates to the tergal plates. The lateral muscles extending from the lateral margins of the definitive sternal plates of the typical abdominal segments consists of two groups, one a short, external, lateral muscle (le), extending to the laterotergite, the other a longer internal muscle (li) extending to the lower region of the tergal plate.

Within the first segment there are two bands of median dorsal longitudinal muscles extending from the intersegmental ridge on the posterior margin of the metathoracic postnotum to the succeeding intersegmental line. A ventral longitudinal muscle (v) extends from the metathoracic furcasternum to the anterior of the intersegmental line between the first and second abdominal sterna. A lateral muscle extends from anterior of the intersegmental ridge dorsally to the posterior margin of sclerite of the first abdominal tergum. Behind this muscle is another smaller lateral

51

muscle (not shown) extending from the lateral intersegmental ridge of the sternum to the intersegmental ridge of the second tergal plate.

The dorsal longitudinal bands of muscle of the second segment are grouped together and not differentiated as median and lateral dorsal longitudinal muscles. A lateral muscle extends from the anterolateral margin of the second sternal segment to a ridge on the ventral region of the third tergal plate. The dorsal, ventral, and lateral muscles of the remaining visceral abdominal segments are typically as described in the outline above, except that the dorsal longitudinal bands of muscle of the seventh segment are grouped together, and in the eighth segment they are hardly differentiated as separate bands of muscle. The ventral longitudinal muscles of the seventh segment are absent. There are no muscles associated with the spiracles.

Musculature of the Female Genitalia and Terminal Abdominal Segments. Two groups of muscles are associated with the first valvifer of the eighth segment. The first (81), probably a modification of the lateral muscles of the visceral segments, originates on the eighth tergal plate and is inserted on a lateral or dorsal apodeme of the first valvifer. The second group (82) consists of short, thick muscles extending from the posterior wall of the first valvifer to the base of the outer ramus of the second valvula and to the anterior wall of the second valvifer. These muscles may be modifications of the ventral longitudinal muscles of the visceral abdominal segments.

Two groups of muscle are associated with the second valvifer, both taking their origin on the ninth tergal plate. The first, a single large muscle (91), is inserted on an anterior apodeme of the lateral, dorsal edge of the second valvifer. The second, consisting of several muscles (92), is inserted on the posterior margin of the second valvifer and the base of the third valvula. In addition there is a short lateral muscle (93) extending from the wall of the apical region of the ninth tergal plate to the caudoventral flap of the ninth tergal plate.

Three small muscles are associated with the tenth segment. These muscles are inserted on the circular margin where the outer, anterior tube and the inner, posterior tube of the tenth segment meet. The first of these (101), inserted mediodorsally on the inner rim of the sclerotized tube of the tenth segment, originates on the dorsal wall of the ninth tergal plate. The second and third muscles (102) are inserted ventrolaterally, and originate on the ventral sides of the ninth tergal plate. These cylindrical sclerites of the tenth segment are apparently incapable of being exserted, telescope fashion, but are limited in their protrusion posteriorly by the membrane between the sclerotized portions of the

ninth and tenth segments. The eleventh segment is probably exserted by the turgidity of the body cavity and the rectum.

Musculature of the Male Genitalia and Terminal Abdominal Segments. The muscles of the male genitalia are surprisingly complex and it would therefore seem likely that the copulation of these insects is no mere approximation of the genitalia of the male with those of the female. It would seem, rather, that considerable maneuvering and adroit procedure on the part of the male is required for the achievement of successful mating.

The internal apodemal process of each paramere bears five distinct muscles. These muscles, all of them paired except the last, are shown in figures 152 and 153 and are as follows:

1. A large muscle (94) extending from the dorsal margin of the anterior region of the apodeme to the lateroventral region of the ninth tergal plate.

2. A second muscle (95) from the dorsal margin of the anterior of the apodeme, lying mesad of the one above, extending to the posterior, or dorsal margin of the basal plate.

3. A muscle (96) extending from the ventromesal margin of the anterior of the apodeme to the anterior margin of the subgenital plate.

4. A muscle (97) extending from the underside of the posterior region of the apodeme to the inner face of the base of the subgenital plate.

5. A single transverse muscle (98, Fig. 153) uniting the anterior regions of the apodemes.

The caudal membranous region of the ninth segment which lies between the base of the aedeagus and the base of the subgenital plate encircles the base of the parameres on each side. This circle of membrane which is formed around the base of the paramere gives rise internally to. a tendon upon which is inserted a fan-shaped muscle (99, Figs. 152 and 153) which originates on the lateral wall of the ninth tergal plate. In addition, a pair of muscles (100), on either side of the median sclerotized process between the aedeagus and the base of the tenth segment, extend to the caudoventral flaps of the ninth tergal plate.

Two pairs of muscles (104, 105, Fig. 153), inserted laterally on the basal margin of the annular sclerite of the tenth segment, have their origins in the dorsal wall of the ninth tergal plate.

THE PHYLOGENY OF AUCHENORHYNCHA

Phylogenetic Considerations of Previous Authors

Concepts of phylogeny, although almost entirely absent in the minds of early nineteenth century insect taxonomists, were nevertheless reflected to some small extent in their systems of classification. Thus, the general relationship of those groups of insects belonging to the Homoptera, and those belonging to the Heteroptera was embodied in Westwood's classification of 1840. Similarly, Dumeril (1806) had indicated the relationship within the Homoptera that existed among the Auchenorhyncha and among those groups later known as the Sternorhyncha. It must be remembered, however, that during the nineteenth century, insect classifications were, like the classifications of other animals, based primarily on one or two key characters, such as the wings and mouthparts. Some success was nevertheless achieved in delineating the ordinal and subordinal relations of insects on this basis, but in attempting to extend the use of one or two key charcters into familial and lesser categories the consequent failure to represent phylogenetic relationship was more evident.

Osborn (1895) took issue with the prevailing system of his day of placing the Coccidae as the lowest and presumably the simplest group of the Homoptera. Separating the Homoptera into two subdivisions, Sternorhynchi and Auchenorhynchi, he claimed that there is every reason to consider the Sternorhynchi as the derivative form and the Auchenorhynchi as the basal form of the phylogenetic tree. He wrote that "The position of the rostrum upon the sternum, or, more properly, the coalescence of the rostrum with the sternum, must certainly be considered as a more specialized condition than the free form and, in fact, the derivative form, the consolidation of the rostrum with sternum being the result of the close approximation of beak and sternum resulting from their food habits."

Within the Auchenorhyncha, Osborn considered the Cicadidae to have the most generalized condition of wing venation and body structure, while the Membracidae, "except in the extremely specialized pronotum are easily seen to be related to the Cicadidae, and naturally take their position next to them. The Fulgoridae, while possessing specializations of the head, are in thoracic structure and venation more generalized than the remaining families, and while possessing many highly differentiated subgroups, may very probably be interposed between the preceding families and the jassoid division. The Cercopidae in development of the

54

scutellum and in texture of elytra, as well as in specialization of the tibiae, show characters of rather high rank, and, if placed as subordinate to the Jassoidea, they must at least be considered as a branch of nearly equal or parallel rank."

Since Osborn utilized such terms as "specializations of the head," "generalized," "characters of rather high rank," "subordinate," "nearly equal or parallel rank," etc. without specific meaning, it is not surprising that his concept of relationships within the Auchenorhyncha, as indicated in Chart 1, was entirely erroneous.
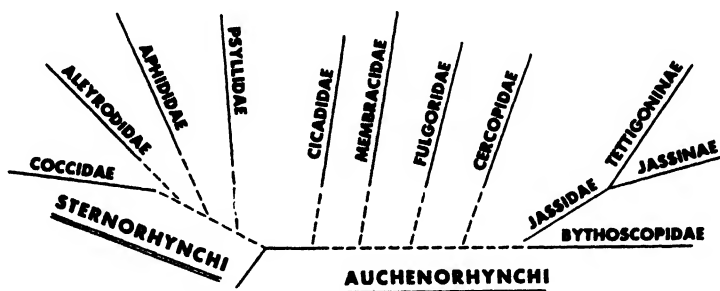
Chart 1. Phylogenetic tree of Homoptera, after Osborn (1895).

Kirkaldy (1910b) pointed out that the interposition of the Fulgoridae between the Cercopidae and the Membracidae is a misconception dating from the earlier studies of Fieber, and was not in the least warranted by the structure or habits of the groups in question. He correctly pointed out that the Fulgoroidea were much more distinct from the rest of the Auchenorhyncha than these latter groups were from each other. In an earlier paper Kirkaldy (1906) concluded that the Fulgoroidea are the "most specialized, highly organized and differentiated" of the Auchenorhyncha, that the Cicadoidea as a whole are of "low estate," and a "slight degree of specialization" is shown by the Tetigonioidea (Jassidae, Membracidae and Cercopidae) in almost every point, and that the Membracidae are only Tetigonioidea with a highly specialized pronotum. His concept of homopteran relationships is expressed in Chart 2.

As to the paleontological evidence, Handlirsch (1908) pointed out that we can follow the Hemipteroids or Rhynchota up to the Paleozoic; that in the Tertiary all essentially modern families were present and even in the Jurassic the principal groups already appear to be marked out, so that we can assign nearly all Mesozoic forms to the orders Homoptera and Hemiptera (Heteroptera). He writes, "As regards the phylogeny of the groups comprised under the Homoptera, it can in any case be maintained, that the present day forms of fulgorids have retained the most primitive characters. They still have, for example, a simply convoluted

intestine without complicated loops (filter chamber), as occur in the jassids and cercopids, etc. Typical fulgorids are already known to us from the Liassic (Lower Jurassic), indeed in that period are also found forms resembling the jassids* and a few species which are inclined toward the cercopids and are consequently designated as Procercopidae. Cicadidae first began to be found in the Cretaceous.
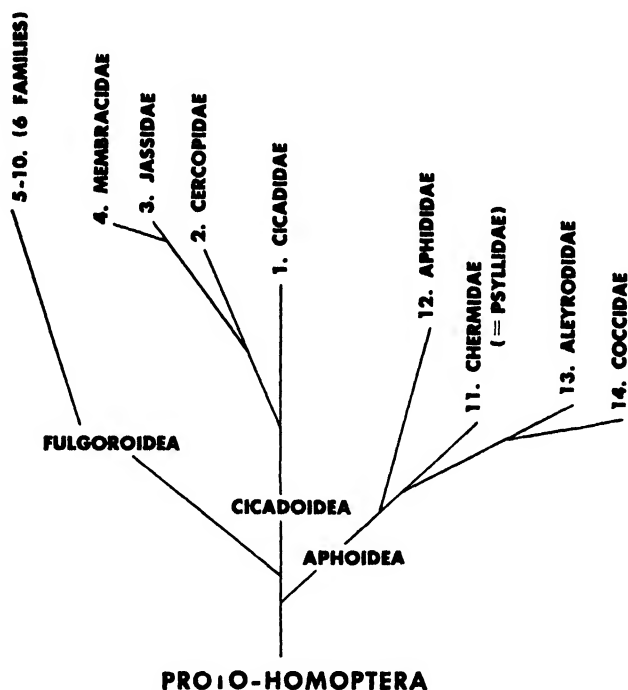
Chart 2. Phylogenetic tree of Homoptera, after Kırkaldy (1910).

"It will not be difficult, to derive the above named families, and the jassids and cercopids as well, from the earlier fulgorids, by the interposition of forms which acquired the characteristic intestinal loops; perhaps these forms were the Proceropidae. The Cicadidae may be derived either from very early cercopids, or also from these Procercopidae, since they too possess the intestinal loops and the characteristic antennae of the families just mentioned. Consequently, I consider the suborder Auchenorhyncha to be a monophyletic, natural one."

The complete line of development including the Sternorhyncha, is, according to Handlirsch, that "From the oldest fulgorids or from the Protohemiptera there developed as early as the Triassic, more specialized

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*Evans (1948) has indicated that "the available evidence would seem to suggest that either true jassoids, or else their immediate ancestors, were in existence during the Permian.

types (perhaps the Procercopidae), from which presumably the jassids and later the cercopids arose, as did the Psylloidea, and from these latter presumably arose the Coccoidea during the Cretaceous. From cercopid-like forms, may have arisen in the Malm (Middle Jurassic), or soon after, the cicadas, while directly from the fulgorids in the course of the Jurassic arose the Aphidoidea, and presumably the Aleurodoidea in the Cretaceous."

In contrast to the Auchenorhyncha, Handlirsch maintained that the Sternorhyncha do not represent a monophyletic group, but a polyphyletic one, and proposed that each of the four families in this group be designated as suborders (though these have superfamily endings), Psylloidea, Aleurodoidea, Aphidoidea, and Coccoidea, of equal rank with the Auchenorhyncha. His interpretation is expressed in the phylogenetic tree shown in Chart 3.
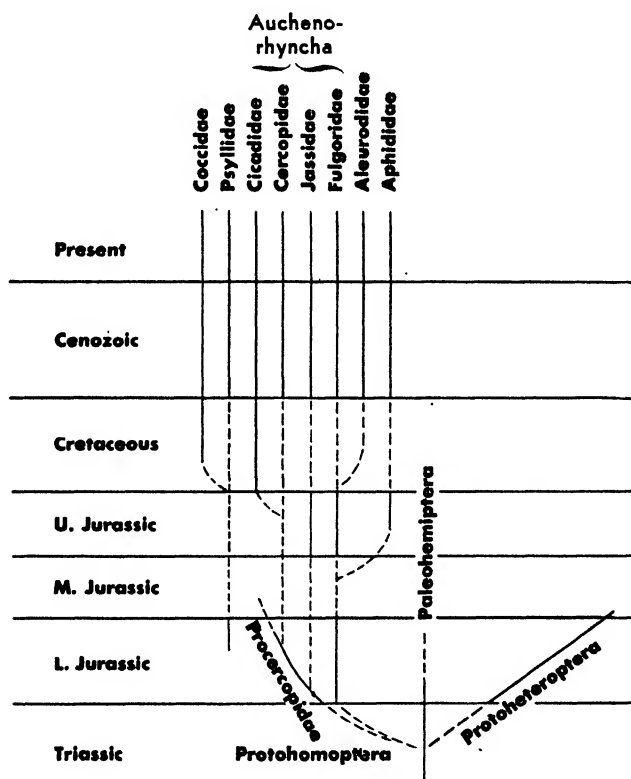
Chart 3. Phylogeny and geological distribution of the Homoptera, after Handlirsch (1908).

Kirkaldy (1910a) took issue with Handlirsch's views on the phylogeny of the Homoptera, particularly as to the derivation of the Aleyrodidae from the Fulgoridae, the placing of both in the same main branch as the

the Aphidae, the separation of all the aforementioned groups from the Psyllidae and the Coccidae, and as to the derivation of the Cicadidae from the Cercopidae, etc. Kirkaldy further disagreed as to the polyphyletic origin of the Sternorhyncha, maintaining that "if there is any group which is apparently compact, it is the Sternorhynchous Homoptera."

Taylor (1918) on the basis of a comparative study of the thoracic sclerites of representative Heteroptera-Homoptera, indicated the following relationships of Homoptera, shown by the thorax, without regard to primitiveness:

Cicadidae......... ⎫ Neuropteroid thorax.... ⎫ Similar thoracic ⎫
Jassidae........... ⎭   ⎬ plan with but few ⎬ Similar
Aphididae............................... ⎭ modifications   ⎭ general
Psyllidae................................   thoracic
Membracidae........Specialized prothorax...................... plan
Cercopidae........ ⎫   ⎭
Fulgoridae......... ⎬ Peculiar fusion of metathoracic
Aleyrodidae........ ⎭ sclerites and coxae....................

Tillyard (1919), in a paper describing fossil Homoptera, consisting of tegmina from the Upper Triassic of Queensland, concluded that "It would appear proved that the Homoptera became differentiated from a single Palaeo-hemipterous stock, of which *Prosbole* is a representative, in the Middle or Upper Permian. From the same stock the Heteroptera became separated off at a somewhat later period, the oldest true Heteroptera known being the Dustaniidae from the Upper Trias of Ipswich. Thus the Homoptera are older than the Heteroptera, as is evident on morphological as well as palaeontological grounds. The separation of the Sternorrhyncha from the Auchenorrhyncha must have taken place before the Upper Trias. The oldest existing family of the Auchenorrhyncha appears to be the Jassidae; the oldest of the Sternorrhyncha are the Psyllidae. Venationally, but not in all other characters, the Jassidae are the older of these two. It may also be pointed out that, after the jassids became differentiated out, the old main stem of the Auchenorrhyncha went on, and continued to be represented by many forms which, *in certain directions,* still preserved archaic characters which the jassids had lost (e.g., the existence of a well developed subcostal vein). Thus there is no difficulty in understanding how the Fulgoroidae and the Cercopidae could have arisen *later in point of time* than the Jassidae, though preserving certain archaic features which the jassids had lost. This is the same problem as that which confronts us in studying the Panorpoid orders, in which it is clear, palaeontologically, that the Mecoptera was the first recent order to be differentiated out, though it is, in some

respects, more highly specialized than other orders which arose from the main panorpoid stem *at later dates,* such as the Megaloptera."

Tillyard's distinction, between one group of insects that may arise later in point of time, but which preserve certain archaic features which an earlier differentiated group has lost, is a most valuable one—even though I consider his evaluation to be incorrect as applied to the fulgorids, cercopids, and jassids. His ideas on phylogeny are expressed in the diagram in Chart 4.
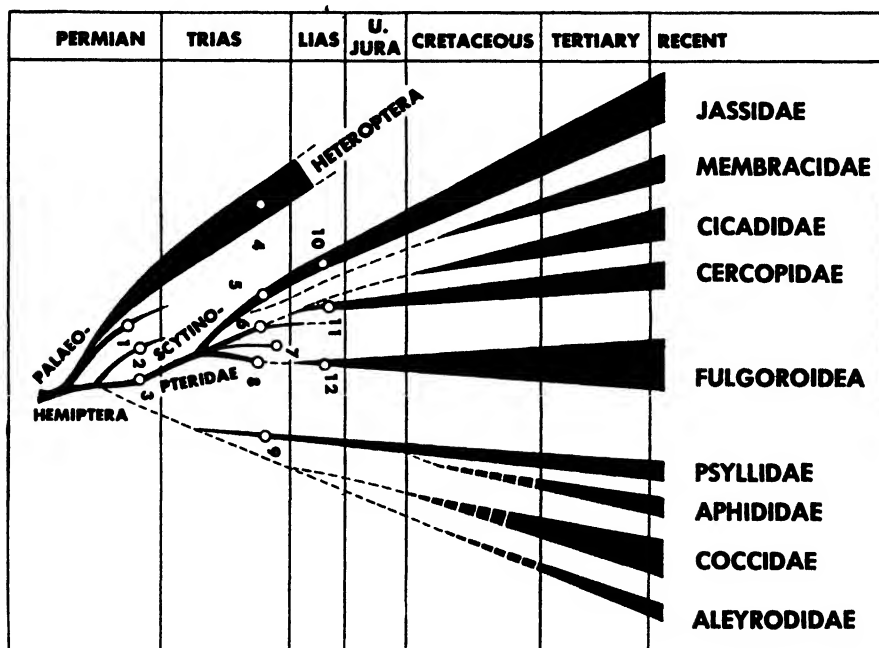
Chart 4. Phylogeny and geological distribution of the Homoptera, after Tillyard (1919). Known fossil types are as follows: 1, *Prosbole;* 2, *Permofulgor;* 3, *Scytinoptera* and *Permoscarta;* 4, *Dunstaniidae;* 5, *Eurymelidium, Mesojassus* and *Triassojassus;* 6, *Mesoscytina, Mesodiphthera* and *Triassoscarta;* 7, *Ipsvicia;* 8, *Mesocixiinae;* 9, *Triassopsylla;* 10, *Archijassus;* 11, *Procercopis;* and 12, *Fulgoridium.*

Singh-Pruthi (1925b), on the basis of an extensive comparative study of the male genitalia of Rhynchota, considered that the "Cicadidae resemble Heteroptera in the form of the VIIIth segment, and in the non-differentiation of the sub-genital plates; the Fulgoroidea also have no sub-genital plates, and moreover, show different grades of aedeagus differentiation parallel to those in Heteroptera. (Still more, most Fulgoroidea, unlike the rest of Homoptera, resemble Heteroptera in not having a complete ovipositor.) But the structure and the position of the basal plates, surrounding the basal foramen or lying on the segmental membrane inside the body cavity, separate the two sub-orders quite dis-

tinctly without any exception. It seems that the heteropterous condition is more primitive, but this cannot be asserted with any certainty unless information about the condition of the basal plates in other orders of insects is available.

"Thus the two sub-orders seem to have a common origin, and are not distinct orders as suggested by some; but they are separated by a good gap, and we must look to palaeontology for some Protohemiptera in which the basal plates are in the intermediate condition."
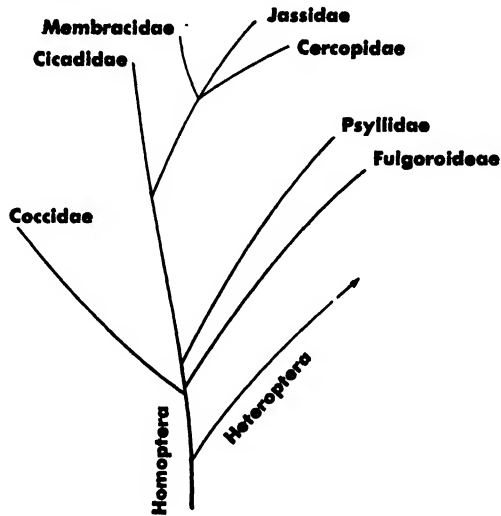
Chart 5. Phylogeny of the Homoptera, after Singh-Pruthi (1925), based on a study of the male genitalia.

Carpenter (1931) described a group of closely related, Lower Permian insects of Kansas, belonging to the fossil family Archescytinidae. He pointed out that the more primitive wing venation of the Sternorhyncha has a reduced anal area and the second anal vein is absent. On the other hand the antennae of Auchenorhyncha, consisting of two short segments plus a bristle or style, are specialized, whereas the antennae of the Sternorhyncha consist of at least three segments and may have as many as twenty-five. As far as the wing venation of the Archescytinidae is concerned, they resemble the Auchenorhyncha, but Carpenter found one species of fossil *Archescytina* which has long antennae consisting of at least twenty-five segments. These insects also have a well developed clavus and three-segmented tarsi, characteristic of Auchenorhyncha. Consequently Carpenter considered that there was hardly justification for placing these Permian insects with the Sternorhyncha, solely on the basis of their antennae. He therefore proposed the erection of a third division, the Paleorhyncha, of equal rank with the Sternorhyncha and

Auchenorhyncha, "in order to avoid abolishing an outstanding char-·
acteristic of the Auchenorhyncha by expanding the definition of that
division to include insects with multisegmented antennae."

Evans (1943) accepted this new division and described a new genus
and species, *Austroscytina imperfecta,* belonging to the Archescyntinidae
within this division, from the Upper Permian of New South Wales. Later
(1948) he pointed out that though it is conceivable that the Archescyn-
tinidae lie close to the line of descent of the Jassoidea, they cannot pos-
sibly have been ancestral to the whole superfamily, since the media of
the tegmen of the Archescyntinidae is invariably three-branched, and
the common ancestor to all the jassoid families must have had a media
with four branches. According to him, the Archescyntinidae may possibly
have been a jassoid family which had already become specialized in cer-
tain directions by Lower Permian times.
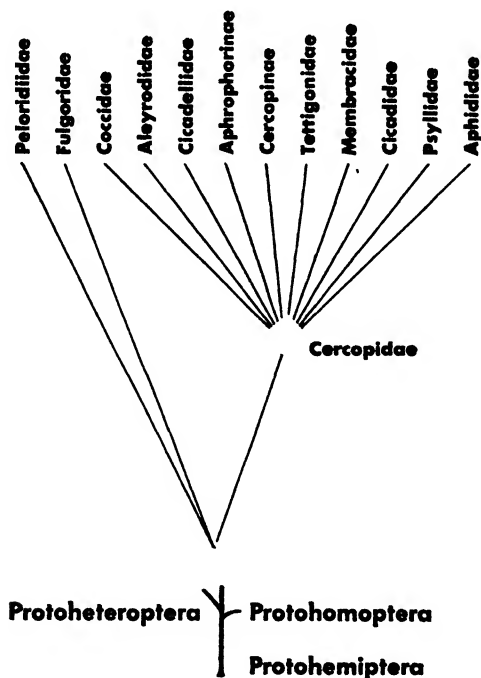
Chart 6. Phylogeny of the Homoptèra, after Spooner (1938), based on a study of
the head capsule.

Spooner (1938), on the basis of extensive comparative studies of the
head capsule of Heteroptera-Homoptera, also recognized the early, dis-
tinctly separate origin of the Fulgoridae from that of other families of
Auchenorhyncha, and derived all the remaining families of both Auchen-
orhyncha and Sternorhyncha from the Cercopidae. His conclusions re-
garding the relationships of the families, arrived at by a study of the
head capsule, are shown in Chart 6.

Evans (1940) agreed with Spooner in the separate derivation of the Fulgoridae and Peloridiidae from the Protohomopterous stem, a suggestion which he himself had previously made (1938), but disputed the derivation of the Sternorhyncha from the Cercopidae and the dual origin claimed for the Jassoidea (Spooner's Cicadellidae and Tettigonidae). He indicated that there was no necessity of attempting to derive either the divisions Auchenorhyncha or Sternorhyncha, one from the other. Further, that while it was reasonable to suggest a dual origin of the Jassoidea on the basis of head structure alone, other characters, such as the wing venation of the hind wings, would not support such a dual derivation. Evans' views (1946) on the classification of the Auchenorhyncha are presented in an earlier section of this paper (p. 4).

The above remarks, concerning the phylogeny of the Auchenorhyncha, indicate that there still exists, among students of the Homoptera, considerable contention regarding the relationships within this division. The palaeontological evidence, while it gives some assistance in determining the age of certain fossil Homoptera and the extent to which certain characters were present in these forms, is comparatively meager and does not, at the present time, substantially improve our knowledge of homopteran phylogeny. Although every source of evidence from this line is to be valued, it is doubtful that our ultimate knowledge of relationship will depend upon this source. Insects are fragile, and to date most of our knowledge of fossil Auchenorhyncha and related forms depends to a large extent, on the fossil wings of Homoptera, or parts of such wings. At best, such evidence is one-sided and not conclusive. Tillyard (1919) in describing fossil Homoptera, based on the tegmina, from the Mesozoic of Queensland, noted "the initial difficulty, that the classification of the Homoptera is based for the most part upon characters other than wing venation" and that although "recent studies of the nymphal tracheation in the various families have much improved our knowledge of the venation,—they have not yielded a really satisfactory basis of classification on venational characters alone."[*]

Discussion

The table (p. 64) summarizes the principal similarities and differences found in the representatives of the *Auchenorhyncha* studied herein. It should be noted first that the species selected to represent the family groups were chosen for availability and not for their primitive position within the family. A conclusive picture of phylogeny cannot be drawn

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[*]Evans stated his belief (in conversation, 1949), based on his own extensive studies, that for the larger categories (families) the venational characters alone do provide a satisfactory basis of classification.

until one has compared the primitive representatives within the families, but to know what is primitive some such investigation as I have made here must be undertaken. Secondly, a series of representatives within the families should ultimately be compared, but such an investigation is beyond the scope of this study. Many of the characters have been compared, however, with other representatives of the families, and with published descriptions. The subsequent remarks will therefore have some worth, even though limited in extent.

The most striking feature of *Scolops pungens* is the primitive nature of all aspects of the sucking pump mechanism in comparison to those of the other Auchenorhyncha. While acknowledging that the sucking pump and stylets of the Auchenorhyncha are in themselves highly specialized mouthparts, those of *Scolops,* and all other fulgorids as far as I know, have remained in a comparatively primitive state of development. To be noted first in this connection are the small proportions of the preoral clypeal area to the remainder of the head capsule (excluding the cephalic head process) in *Scolops,* compared to the much greater proportions of this area in the cicada, the cercopid, the cicadellid, and the membracid. Figure 8a, representing the lateral view of the head capsule of an undescribed species of *Scudderia* (Orthoptera), has been drawn for comparison with the essentially orthopteroid proportions of the clypeal area to the remaining head capsule in *Scolops pungens* (Compare with Figs. 18, 30, 40, and 49).

In connection with the primitive nature of the sucking pump mechanism in *Scolops pungens,* it should be noted that the mandibular and maxillary stylets both bear single protractor and retractor muscles. In the other forms the musculature is always more complex, there being two or three retractor muscles, and frequently additional protractor and retractor muscles associated with the lever of the maxillary stylet as well as with the stylet itself. There is no evidence, as far as I have been able to ascertain, that the fulgorids have ever developed a sucking pump mechanism comparable to that found in other Auchenorhyncha. It seems sound to assume that the other Auchenorhyncha must have at one time passed through a stage in which the sucking pump mechanism was in a similar, relatively undeveloped state.

The ovipositor of *Scolops pungens* also represents an exceedingly primitive stage of development. Particularly to be noticed is the vertical position and lack of differention of the first and second valvifers and the ramal plate (Fig. 131). In contrast, the valvifers and ramal plate of *Tibicina, Lepyronia, Aulacizes,* and *Ceresa* are considerably modified, their position having shifted in a strongly marked, diagonal, anteroventral direction, and the first and second valvulae are highly specialized. The

	Scolops pungens (Fulgoridae)	*Tibicina septendecim* (Cicadidae)	*Lepyronia quadrangularis* (Cercopidae)	*Aulacizes irrorata* (Cicadellidae)	*Ceresa bubalus* (Membracidae)
Clypeus and sucking pump	Comparatively little developed	Well developed	Well developed	Well developed	Well developed
Frenum	Part of clypeus. Connected to hypopharynx by narrow bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge	Distinct. Connected to hypopharynx by wide bridge
Ocelli	Two	Three	Two	Two	Two
Antennae	Below eyes. Enlarged pedicel	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged	Between eyes. Pedicel not enlarged
Labium	Elongated. Paired posterior plates second of 4 segments	Elongated. Paired posterior plates middle of 3 segments	Short. Paired posterior plates absent	Short. Paired posterior plates* at base of apical segment	Short. Paired posterior plates at base of apical segment
Musculature of stylets	Single protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles	Multiple protractor and retractor muscles
Tentorium	Posterior tentorial bridge only	Dorsal, anterior arms, and bridge connected	Dorsal, anterior arms, and bridge connected	Anterior arms reduced	Anterior arms absent
Tegula	Present	Absent	Absent	Absent	Absent

Wings	Forewing tegmen-like; hindwing membranous	Both wings membranous	Forewing tegmen-like; hindwing membranous	Forewing tegmen-like; hindwing membranous	Both wings membranous
Nodal line	Absent	Present	Absent	Absent	Absent
Pleural wing groove	Absent	Absent	Present	Present	Present
Metathoracic coxa and epimeron	Fused	Distinct	Meron articulates with epimeron	Distinct	Distinct
Basal tarsal segments of hind leg	Apical margins spined	Not modified	Apical margins spined	Apical margins spined	Not modified
Pulvillus	Single median lobe	Absent	Notched medially	Bilobed	Bilobed
Hind tibia	Single row of spines	Four spines	Two large spines	Four rows of spines	Four rows of spines
Abdominal spiracles	Between tergites and laterotergites	Ventral margin of tergites	Ventral margin of laterotergites	Ventral margin of laterotergites	Ventral margin of laterotergites
Ovipositor	Primitive	Specialized	Specialized	Specialized	Specialized
Male subgenital plates	Absent	Absent	Present	Present	Present
10th & 11th abdominal segments	10th—flat; 11th telescoped	10th & 11th telescoped	10th & 11th telescoped	10th and 11th telescoped	10th & 11th telescoped

*The suggested glossae of Evans (1937).

primitive nature of the ovipositor and the sucking pump, taken together with the simple, unconvoluted condition of the intestinal canal reported for the Fulgoridae by Handlirsch (developed into the specialized "Filter chamber" in the remaining auchenorhynchous families), would indicate to the writer that the Fulgoridae is a group which is distinctly separate from all other Auchenorhyncha, and was the earliest to be differentiated from the common base of the Auchenorhyncha.

Other characters which separate the Fulgoridae from the remaining families are the fusion of the meron of the coxa of the metathoracic leg with the epimeron, and the greatly modified second segment of the antenna. These characters, however, represent specializations rather than primitiveness. The Fulgoridae are also distinct in the possession of a tegula, absent in other Auchenorhyncha, as far as I have been able to ascertain.

Before proceeding further, it would be well to point out that the ovipositor of *Scolops pungens* is considerably more primitive than that found in many representatives of the Orthoptera, which group has mandibulate mouthparts. Thus we can see that within two distinct orders we have a combination of both primitive and specialized characters. The more primitive mandibulate mouthparts are combined with highly specialized ovipositors in many groups of Orthoptera, whereas the fulgorid combines specialized sucking mouthparts (compared to mandibulate mouthparts) with a primitive ovipositor. This should make it clear that insects by themselves are neither primitive nor specialized, and that these terms can only be applied in a true, comparative sense to the individual parts of insects. The fulgorids, for example, have been referred to by some authors as being primitive insects, by others (Kirkaldy, 1906; Funkhouser, 1917) as being specialized. Such terms offer no guide to phylogeny, for it is an evaluation of separate characters which is important in the interpretation of relationships.

There has been considerable controversy concerning the origin of the loral areas. Snodgrass (1938), in supporting his theory that the lorum is derived from the hypopharynx, suggested that the loral areas in the Fulgoridae represent a specialized, rather than a generalized condition. In view of the fact that the clypeal, sucking pump region of the fulgorid is a primitive one, in comparison with other Auchenorhyncha, it would support the contrary concept that the outer part of the lorum is differentiated from the lateral area of the clypeus, rather than from the hypopharynx. Attention is called to the narrow lateral arm of the hypopharynx (la, Figs. 9 and 10) which connects to the lorum. It seems likely that this narrow arm between the hypopharynx and the lorum has been differentiated from the hypopharynx, and has apparently expanded, in the

other families of Auchenorhyncha, to form the broader connection. Thus it might well be that although the loral areas are derived mainly from the lateral regions of the clypeus, a part of the hypopharynx has formed a bridge with the present structure.

The relationships and origins of the remaining groups of Auchenorhyncha is a much more difficult matter. Much of the difficulty arises from the fact that when we consider the Cicadidae, Cercopidae, Cicadellidae, and Membracidae, we tend to think in terms of the numerous, recent representatives of these groups. These recent representatives have a number of characteristics which, taken together, mark these families off distinctly. Thus, the cercopid, cicadellid, and membracid possess an unmistakable similarity in the general plan of the thoracic sterna which links these three forms together, and differentiates them from the cicada. No doubt this similarity of the thoracic sterna is correlated with another distinguishing feature, the presence of jumping hind legs, which separates the Cercopidae, Cicadellidae, and Membracidae from the Cicadidae. In addition, the head of Cicadidae retains a small fronslike area bearing a median ocellus, absent in Cercopidae, Cicadellidae, and Membracidae. It should be pointed out, too, that the loral areas lie alongside the entire length of the postclypeus in the cicada, clearly the more ancestral condition as indicated in the fulgorids, whereas in the cercopid, cicadellid, and membracid, the upper portions of the lorae are folded into the head capsule or reduced, so that they are seen to lie adjacent to the ventral portion of the postclypeus only. All these characters suggest that the Cicadidae are distinct from the Cercopidae, Cicadellidae, and Membracidae.

In this connection attention is called to the pleural wing grooves, present in *Lepyronia, Aulacizes,* and *Ceresa,* which enable the bases of the anterior margin of the tegmina to lock in place when at rest. This device is absent in *Tibicina.* If such structures are consistent within Cercopidae, Cicadellidae, and Membracidae, they may represent another reason for grouping these families apart from the Cicadidae.

Of these remaining three groups, the Cercopidae alone possess a complete tentorium in which the anterior tentorial arms are connected with the posterior arms (as is also the condition in the Cicadidae), whereas in both the Cicadellidae and Membracidae the tentorial structure is reduced; the anterior arms no longer retain a connection with the posterior arms. The hind legs of both Membracidae and Cicadellidae bear spines, which are absent on the hind legs of Cercopidae. Evans (1946a) has recognized these affinities in grouping membracids and cicadellidids in one superfamily, Jassoidea, as distinct from the Cercopoidea. In addition the thoracic sterna of *Aulacizes* and *Ceresa* are exceedingly similar and both

possess a differentiated, mesothoracic antecoxal area (acx$_2$, Figs. 69 and 74), absent in *Lepyronia*.

It should be pointed out that a similar tendency toward the reduction of the tentorial structure, already accomplished in the Cicadellidae and Membracidae, is present also in the Fulgoridae. Although most members of the Fulgoridae possess anterior tentorial arms, and in some the dorsal tentorial arms are also present, the tentorial structure is reduced to the posterior tentorial bridge in *Scolops*. The antennal muscles, normally inserted on the dorsal tentorium in many insects, are here inserted on the posterior tentorial bridge. This tendency toward the development or reduction of particular structures within separate phylogenetic lines of the Auchenorhyncha is a widespread one. We thus find that although the modern representatives of these auchenorhynchous groups are sufficiently distinctive and readily defined, certain more primitive representatives show a remarkable number of features in common, and it is for this reason that any attempt to determine when these familial groups originated in point of time is such a difficult one.

The epistomal suture, lacking in some cercopids, the majority of present-day jassids, and most membracids, is nevertheless present in some representatives of all of these groups as well as in the fulgorids and cicadas. The subgenal, or maxillary, suture, found in some of the fulgorid representatives of this study, is completely present in some jassids (Ulopinae and Stenocotini), and is vestigial in the primitive cicada, *Tettigarcta*, some cercopids, and some jassids. It is absent only in membracids. Further, Evans (1948) pointed out that the basic membracid type of tegminal venation,[*] as represented by *Xiphistes tuberculatus*, closely resembles the jassid type and differs only in that M is not fused basally with R, and that probably the oldest representatives of the membracids go back to very early times. This basic membracid tegmen closely resembles Evans' (1946a) reconstruction of the hypothetical, ancestral tegmenal venation of the Jassoidea (Evans' families Aetaleonidae, Hylicidae, Eurymelidae, and Jassidae). Only when we consider the more recent groups do we find specializations which are of recent origin. Another character thought to be confined to the family Cicadidae, namely the transverse nodal line of the tegmina, has been found in the jassoid family Hylicidae. Apart from the Hylicidae, no trace of such a line is retained in any other jassoids.

. Additional evidence along these lines has recently been brought forth in the interesting studies of Ossiannilsson (1949), who pointed out that

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[*]According to Evans the arrangement of the veins of the tegmen offers a more reliable character for the determination of relationships within the Membracidae, than those of the highly variable pronotum (a much more recent specialization), heretofore relied upon.

the tymbal organs of Homoptera, generally considered to be present only in the Cicadidae, are also present in cercopids, membracids (*Centrotus*), some jassoid forms, and the fulgorid, *Ommatidiotus*. In cercopids and certain jassoid genera the female possesses a functional sound-producing organ of the same type as that of the male, though weaker. Moreover, the female of *Paropia* has a distinctly striated tymbal which is, in the male, only represented by traces. In *Doratura* both sexes have a sound-producing organ of the same type and equally well developed. Ossiannilsson suggests that primitively both sexes possessed practically identical tymbal organs, and that the present condition, wherein these organs are usually confined to the males, has been brought about by reduction. He concluded that the possession of a functional tymbal apparatus is general among the Auchenorhyncha.

Evans (1940b) has called attention to the fact that not only the nymphs of cicadas, but those of many cixiids (Fulgoridae) and certain cercopids are subterranean, and that this may well be a primitive characteristic, possibly associated with severe weather conditions prevailing at some past period of geological history. The study of the habits and behavior patterns of Auchenorhyncha is an almost unexplored field for the investigator and, if studied from the comparative point of view, could undoubtedly contribute much additional evidence to the solution of problems of relationship.

All of this evidence supports the contention that only the numerous modern representatives of the Cicadidae, Cercopidae, Jassidae, and Membracidae are distinct and well defined; and that there are an impressive number of instances in which primitive, less numerous, and little known representatives of these groups show a variety of characters in common.

It is interesting to note that the meso- and metathoracic segments of *Tibicina septendecim* and *Ceresa bubalus* show certain superficial resemblances of shape and structure, as well as fore- and hindwings which are both membranous. I have already pointed out that the affinity of the membracid thorax lies with that of the cicadellid, and to a somewhat lesser extent with that of the cercopid.

Lawson (1922) suggested that the main branch of the Cercopidae arose a little earlier than that of the Cicadellidae and Membracidae, based on the assumption that spittle-mass production must have required a long time to perfect. Although there is morphological, and perhaps palaeontological, evidence which might support an earlier origin of the Cercopidae, such an earlier origin is not, in my opinion, supported by the development of a specialization such as spittle-mass production. This is

but one example of the difficulties inherent in the attempts to reason out phylogeny.

It is difficult to say whether there have been two "main" divisions of development or three as Evans (1946) has recently suggested. If we are to accept three, I would consider that the Cicadomorpha (Cicadidae) and Jassidomorpha (Cercopidae, Cicadellidae, and Membracidae) are more distinctly separated from the Fulgoromorpha (Fulgoridae) than they are from each other, while acknowledging that the Cicadidae do show distinct differences from the Cercopidae, Cicadellidae, and Membracidae. The Fulgoridae were the earliest group to be differentiated from the base of the auchenorhynchous stem, and are clearly distinct from the remaining Auchenorhyncha. The cercopids, cicadellids, and membracids are closely related, and the latter two groups show very marked affinities. On the basis of this study, and our present knowledge of cicadas on the one hand and the cercopids, cicadellids, and membracids on the other, the writer finds no conclusive evidence to support an earlier origin for one or the other of these groups. Evans, however, has stated (in conversation) that the modern cicadas were probably differentiated earlier than modern jassids, but that the jassoid stem originated at an earlier date than the cicadoid stem. As additional, primitive representatives of these groups come to light, we may be able to make more valid conjectures concerning their probable origin in time.

No attempt has been made to evaluate the taxonomic categories used in this discussion. The family names have been used to indicate broad groups and their general relationship. It is very likely that superfamily and subfamily designations may properly replace certain family groups as various writers have already suggested.

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71

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LIST OF ABBREVIATIONS

1A   —1st anal
2A   —2nd anal
3A   —3rd anal
aclp —anteclypeus
acs —antecostal suture
acx —antecoxal area
aed —aedeagus
aepm —anepimeron
aes —anepisternum
an   —anus
anp —anterior notal wing process
ant —antenna
as   —anal style
at   —anterior tentorial arm
atp —anterior tentorial pit, or invagination
au   —auditory capsule
aw   —prealar bridge
1ax —first axillary sclerite
2ax —second axillary sclerite
3ax —third axillary sclerite
ba   —basalare, or basalar sclerite
bcx —basicoxite
bp   —basal plate
br   —brain
bst —basisternite
C   —costa
cl   —claw, or ungue
clr —clypeal ridge, or apodeme
cx   —coxa
cxp —pleural coxal process
Cu   —cubitus
d   —dorsal longitudinal muscle
dc   —dorsal cervical sclerite
dl   —lateral dorsal longitudinal muscle
dm   —median dorsal longitudinal muscle

dlclp —dilator muscles of the clypeus
dsyr —dilator muscle of the salivary syringe
dt   —dorsal arm of the tentorium
e   —compound eye
epm —epimeron
eph —epipharynx
es   —episternum
est —epistomal suture
fe   —femur
fl   —flagellum of the antenna
fp   —furcal pit
fr   —frons, or frontal region
fst —furcasternite
fu   —furcal apodeme
ge   —gena, or genal region
gnp —gonopore
gp   —subgenital plate
ha   —humeral angle of pronotum
hph —hypopharynx
hwp —hypopharygeal wing plate
is   —intersegmental line
jf   —jugal fold
kepm —katepimeron
kes —katepisternum
l   —lateral abdominal muscle
lb   —labium
lc   —lateral cervical sclerite
le   —external lateral abdominal muscle
lh   —lateral arm of hypopharynx
li   —internal lateral abdominal muscle
lm   —labrum
lor —lorum
ltg —laterotergite
lvr$_1$ —lever of the mandibular stylet

76

lvr_2 —lever of the maxillary stylet

M —media

mant —antennal muscle

mds —mandibular stylet

mlb —muscle of the labium

mm —muscle maculum, or marking

mp —muscle partition formed by apodemal wall of pronotum

mr —meron of coxa

ms —median suture of metathoracic scutum

mtp —metopidium of pronotum

mxp —maxillary plate

mxap —apodemal plate of the maxillary

nl —nodal line of wing

oc —ocellus

occ —occipital condyle

ocn —ocellar nerve

opc —operculum

opn —optic nerve

pc —precosta, or pretergite

pclp —postclypeus

pdc —pedicel of the antenna

ph —phragma

plap —pleural apodeme

plb —protractor muscle of the labium

pls —pleural suture

pm —paramere

pmds —protractor muscle of the mandible

pmp —sucking pump

pmxs —protractor muscle of the maxillary stylet

pnp —posterior notal wing process

pnt —postnotum

pocx —postcoxal bridge

prnt —pronotum

psc —prescutum

ptp —posterior tentorial invagination

pu —pulvillus

pw —postalar bridge

R —radius

rd —reduplication of scutellum

1ri —inner ramus, or sclerotized thickening, of first valvula

rlb —retractor muscle of the labium

rmds —retractor muscle of the mandibular stylet

rmxs —retractor muscle of the maxillary stylet

1ro —outer ramus, or sclerotized thickening, of first valvula

2ro —outer ramus, or sclerotized thickening, of second valvula

rp —ramal plate

Is, IIs. etc. —first abdominal sternite, etc.

Sc —subcosta

sc —scutum

scl —scutellum

scp —scape of the antenna

sgng —subesophageal ganglion

sgs —subgenal suture

sh —suprahumeral horn of pronotum

sld —salivary duct

slg —salivary glands

sp —spiracle

syr —salivary syringe

It, IIt, etc. —first abdominal tergite, etc.

ta —tarsus

tb —posterior tentorial bridge

tg —tegula

$thgng_1$ —prothoracic ganglion

ti —tibia

tn —trochantin

tr —trochanter

ts —tergal spine

twg —tergal wing groove

tyb —tymbal

typ —tympanum

unp —unguitractor plate

v   —ventral longitudinal muscle

vc   —ventral clasper of 10th segment

vf   —vannal fold

1vl   —first valvula

2vl   —second valvula

3vl   —third valvula

1vlf   —first valvifer

2vlf   —second valvifer

vst   —vestibulum

vx   —vertex

I, II, etc.—first abdominal segment, etc.

PLATES WITH EXPLANATIONS

PLATE I

1. Lateral view of head of *Acalonia* sp.
2. Frontal view of head of *Acalonia* sp.
3. Frontal view of head of *Ormenis pruinosa* (Say)
4. Lateral view of head of *Ormenis pruinosa*
5. Frontal view of head of *Epitera septentrionalis* Say
6. Frontal view of head of *Oliarus aridus* Ball, with maxillary lobes displaced
7. Frontal view of head of *Scolops pungens*
8. Lateral view of head of *Scolops pungens*
8a. Lateral view of head of *Scudderia sp.* (Orthoptera)
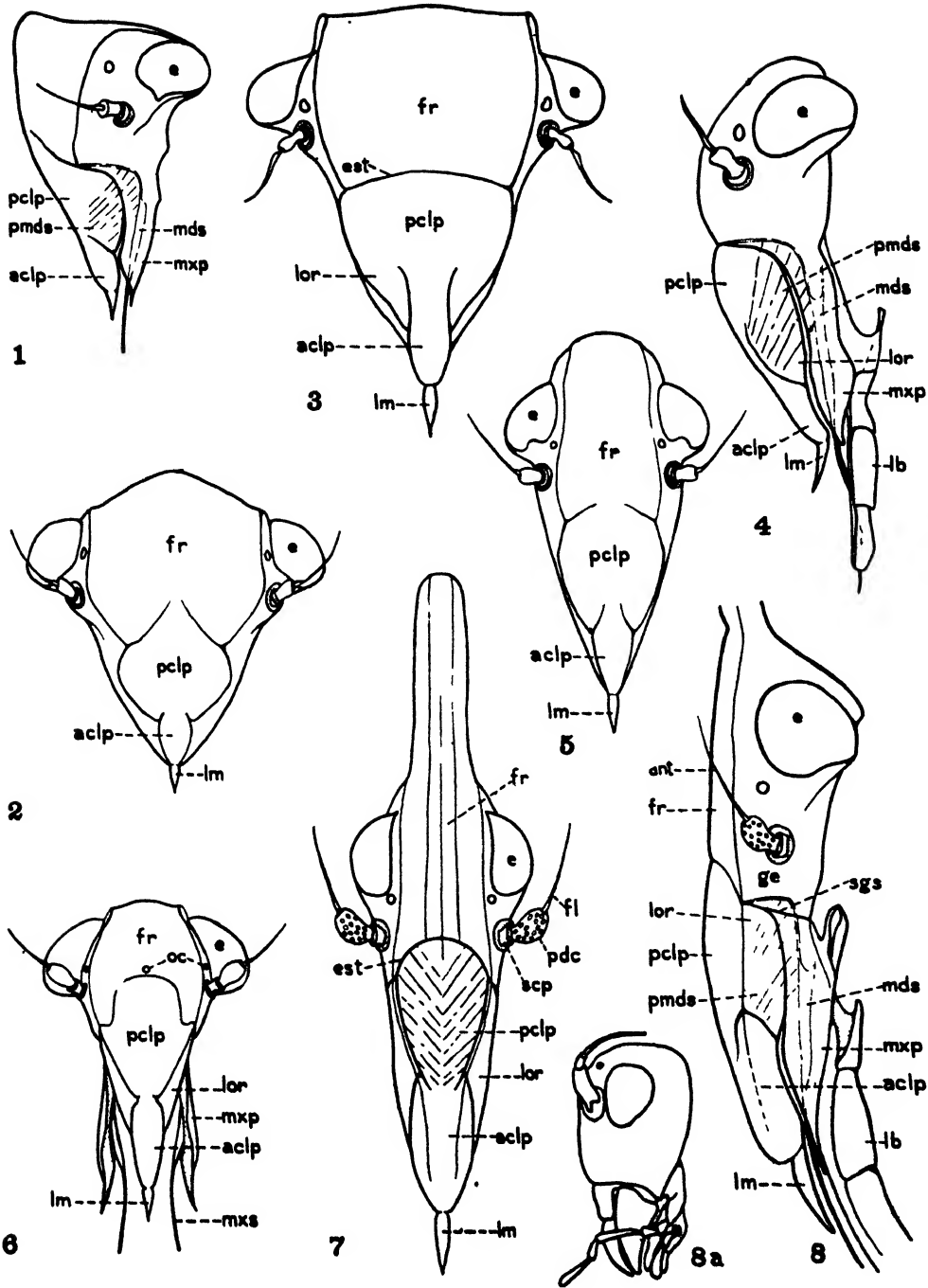
PLATE II

9. Sagittal section of lower part of head of *Scolops pungens*, showing attachment of hypopharynx to the head capsule

10. Anterior views of hypopharynx of *Scolops pungens*

11. Posterior view of hypopharynx, maxillary plate and posterior tentorial bridge of *Oliarus aridus*

12. Muscles and articulation of right mandibular stylet of *Scolops pungens*

13. Sagittal section of the head of *Scolops pungens*

14. Median section of labium of *Scolops pungens*

15. Muscles and articulation of right maxillary stylet of *Scolops pungens*

16. Posterior view of head of *Scolops pungens*, with labium removed

17. Posterior view of labium of *Scolops pungens*
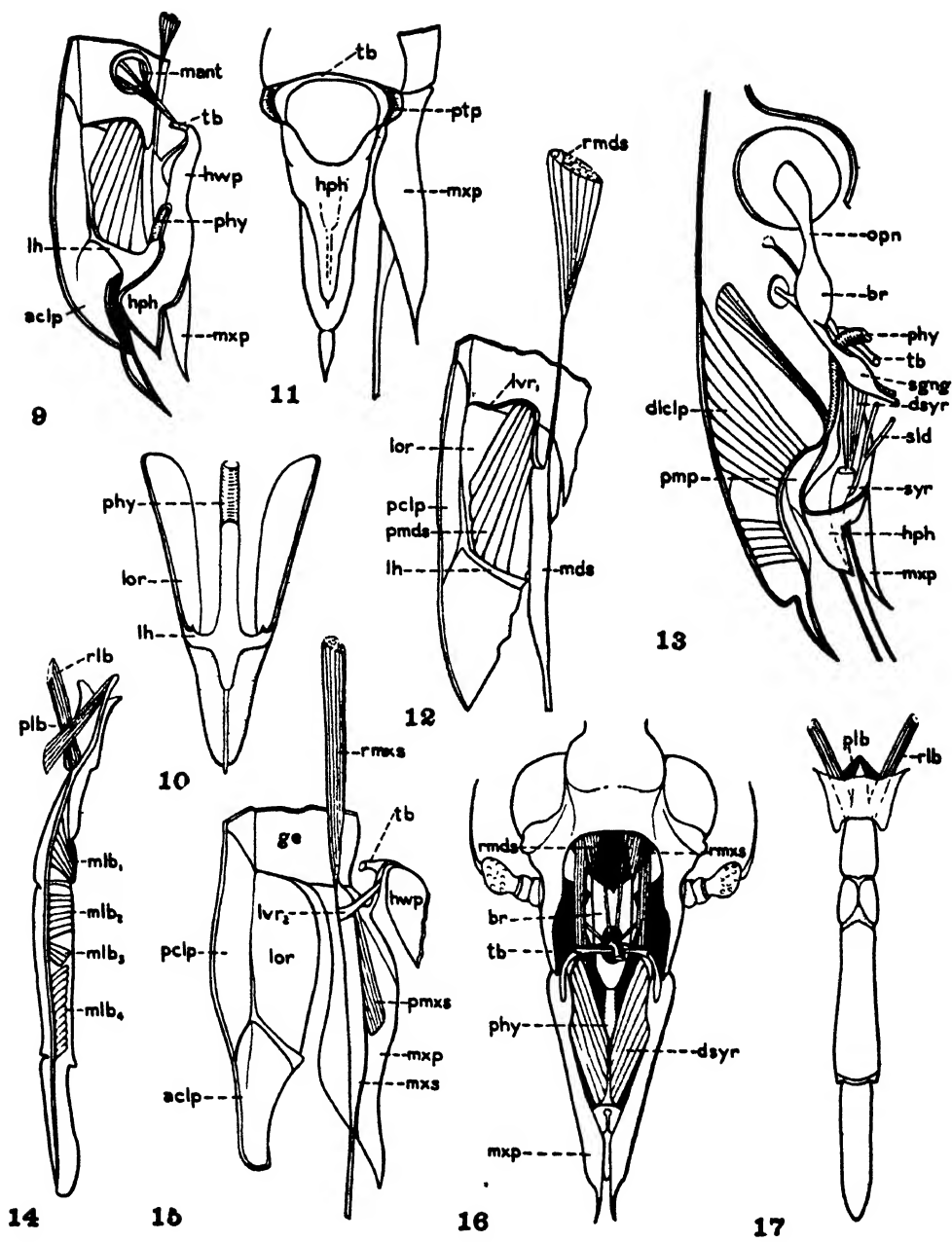
PLATE III

Tibicina septendecim

18. Sagittal section of head
19. Anterior view of head
20. Posterior view of hypopharyngeal wing plate
21. Lateral view of labium
22. Median section of basal segments of labium
23. Muscles of the maxillary stylet
24. Cross section of head through hypopharynx, sucking pump, and post-clypeus
25. Posteroventral view of tentorium and hypopharyngeal wing plate of upper right half of head
26. Dorsal view of head
27. Posterior view of head, with labium removed
28. Muscles of the mandibular stylet

PLATE V

Aulacizes irrorata

38. Anterior view of head
39. Dorsal view of head
40. Sagittal section of head
41. Posterior view of head
42. Muscles and articulation of the maxillary stylet
43. Lateral view of labium
44. Median section of labium
45. Cross-section of head through hypopharynx, sucking pump and post-clypeus
46. Posterior view of internal section of head showing the articulation and muscles of the mandibular stylet
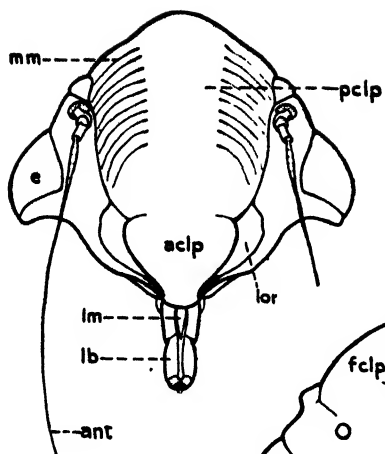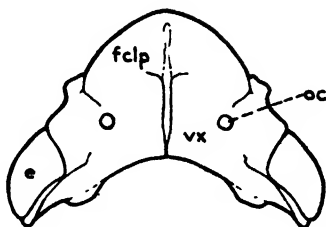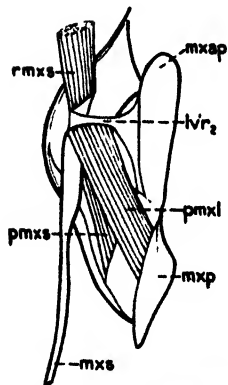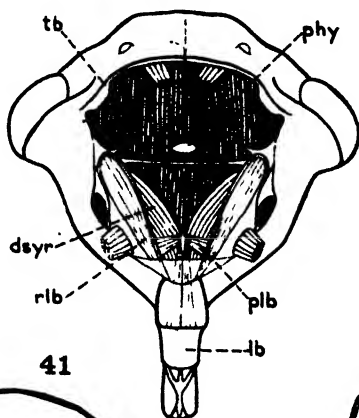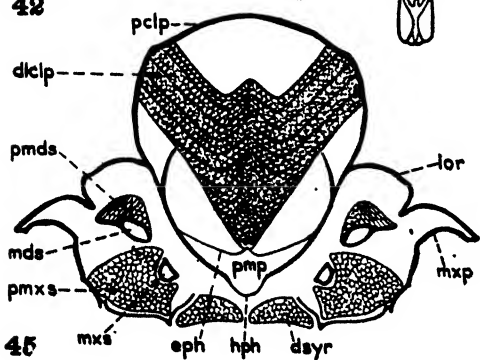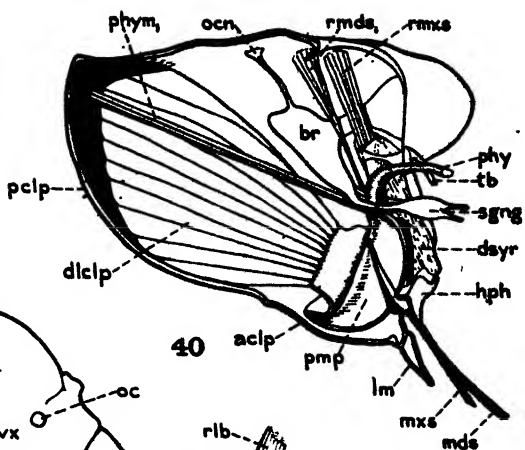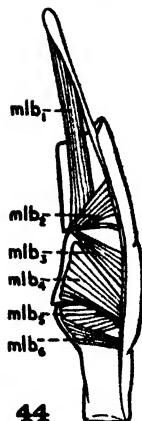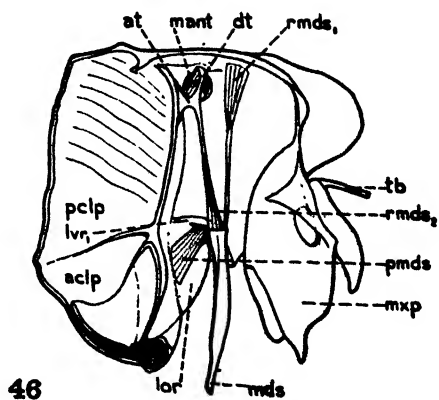
PLATE VI

Ceresa bubalus

47. Ventral view of head
48. Anterior view of head
49. Sagittal section of head
50. Posterior view of head
51. Lateral view of labium
52. Median section of labium
53. Articulation and muscles of maxillary stylet
54. Sagittal section of head, showing articulation and muscles of mandibular stylet

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rmxs   21

occ   22 23

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hph   dsyr

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mds

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mlb₄

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plb

rmxs

tb   hwp

lvr₂

pmxl

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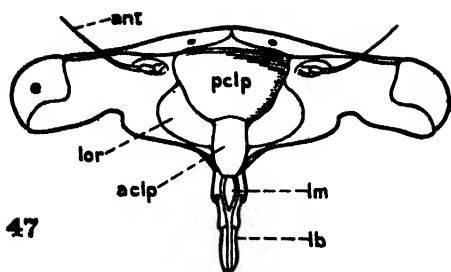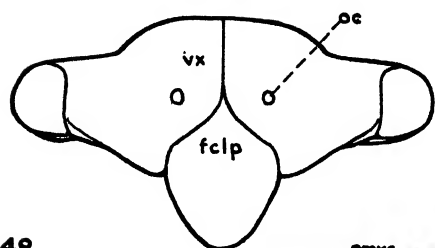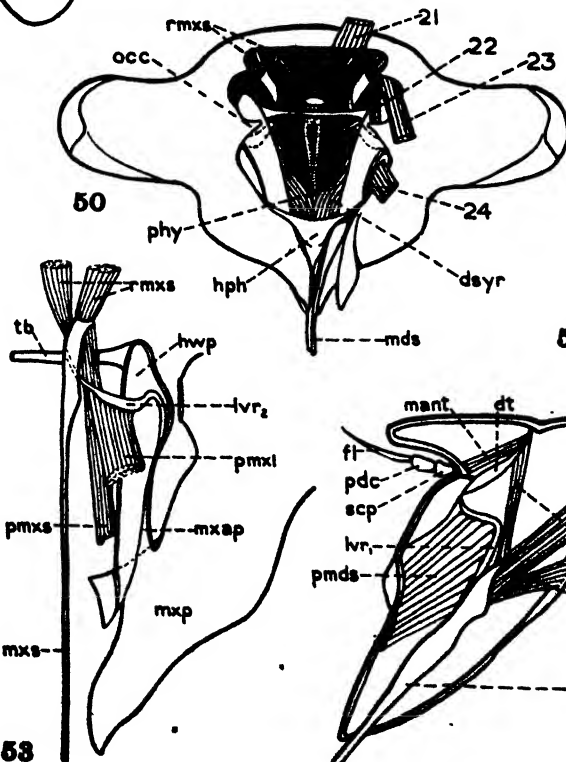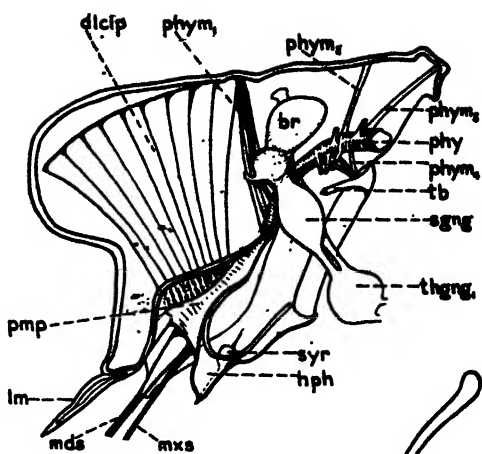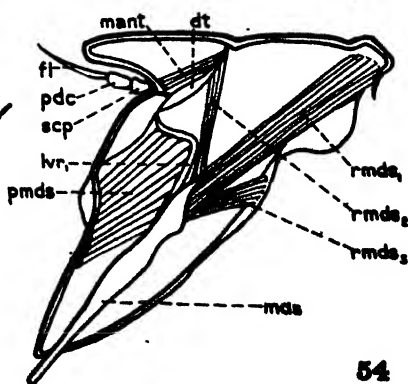
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PLATE VII

55. Lateral view of thorax of *Scolops pungens*
56. Dorsal view of thorax of *Scolops pungens*
57. Dorsal view of thorax of *Tibicina septendecim*
58. Lateral view of thorax of *Tibicina septendecim*
59. Dorsal section through intersegmental area of pro- and mesothoracic segments of *Tibicina septendecim*
60. Ventral view of thorax of *Scolops pungens*
61. Ventral view of thorax of *Tibicina septendecim*
62. Posterior view of phragma between meso- and metathoracic segments of *Tibicina septendecim*
63. Posterior view of prothoracic endoskeleton of *Scolops pungens*
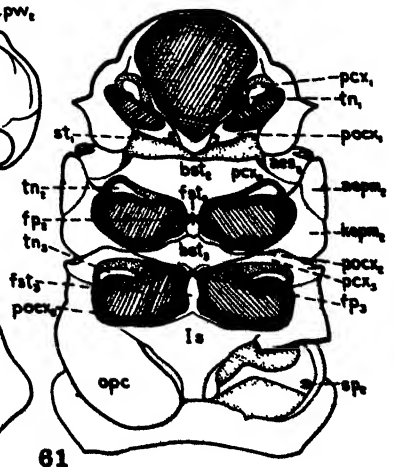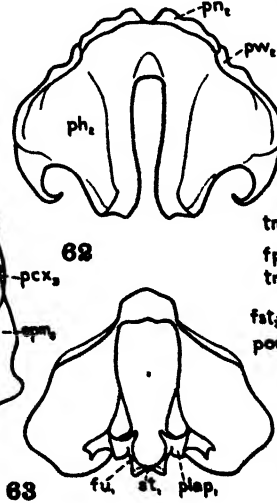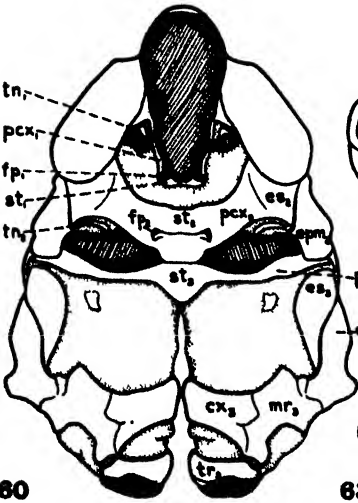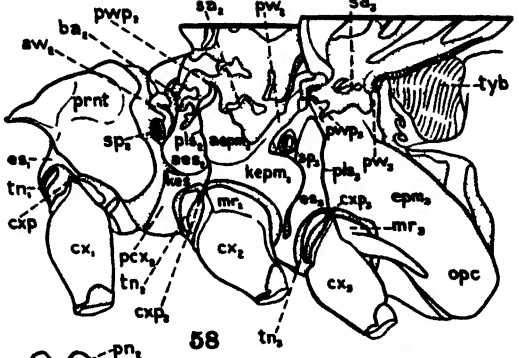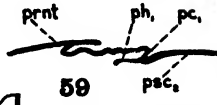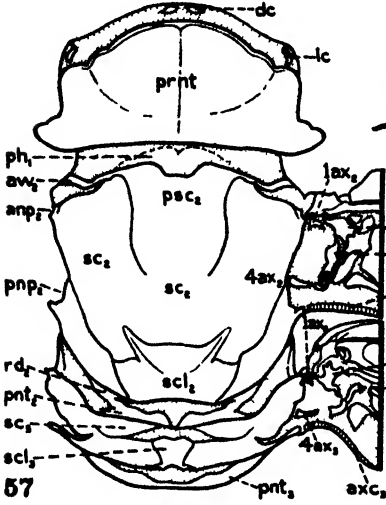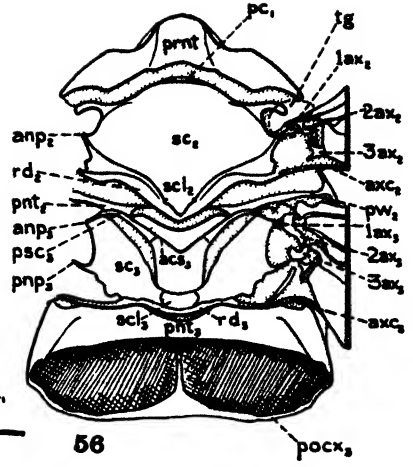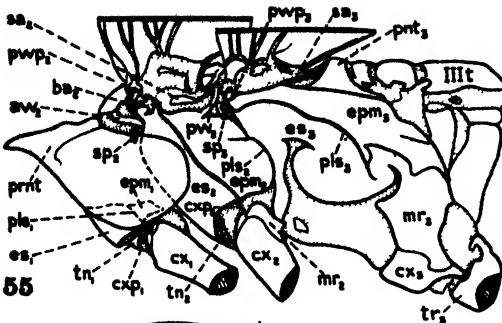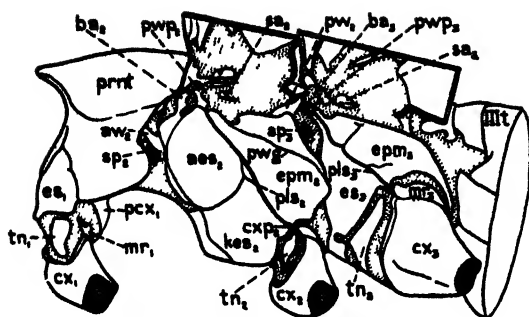
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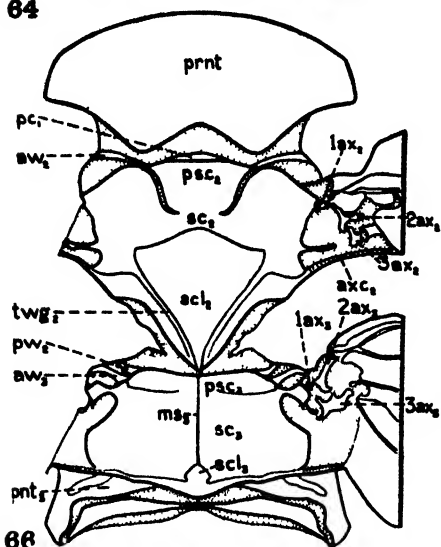
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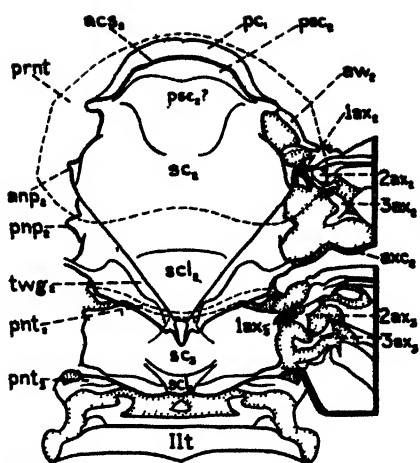
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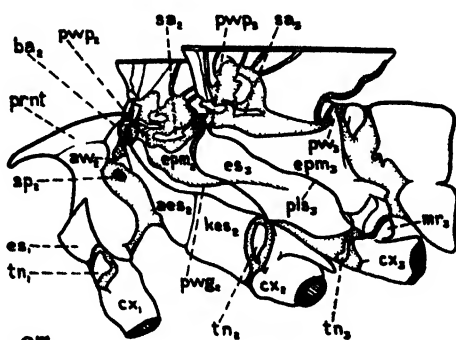
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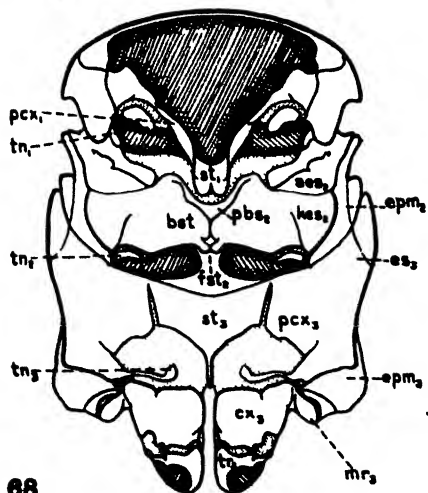
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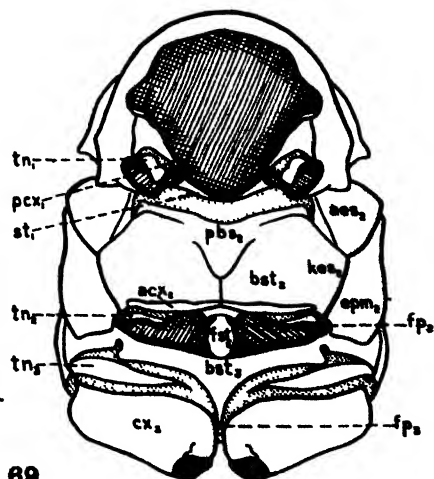
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PLATE IX

Ceresa bubalus

70. Dorsal view of meso- and metathoracic segments
71. Ventral view of meso- and metathoracic segments
72. Posterior view of prothorax
73. Posterior view of metathorax
74. Ventral view of thoracic segments
75. Anterior view of prothorax
76. Anterior view of metathorax
77. Posterior view of endoskeleton of mesothorax
78. Anterior view of mesothorax
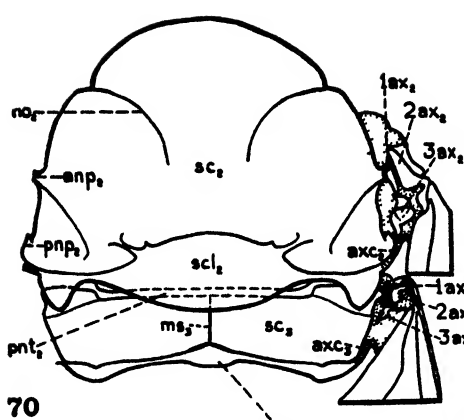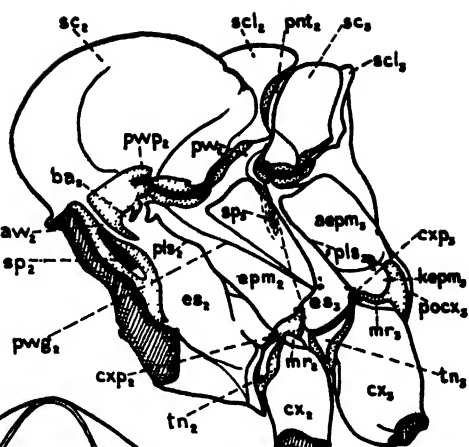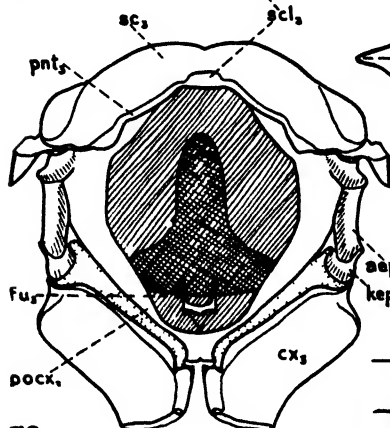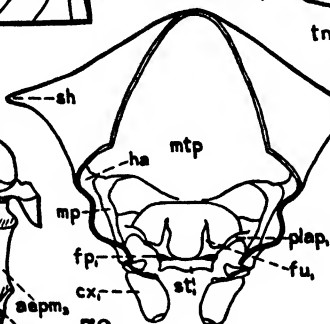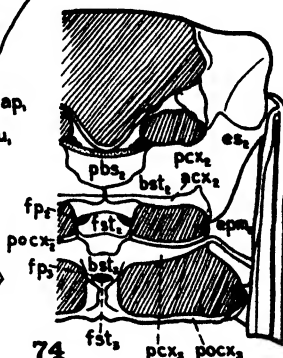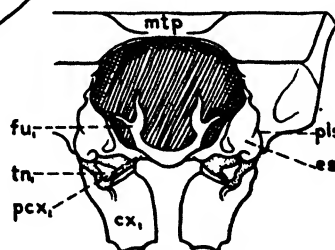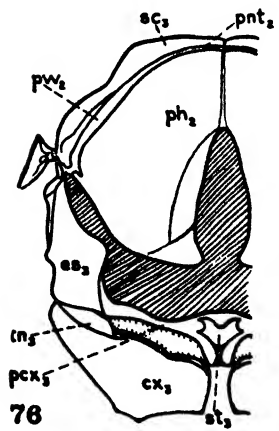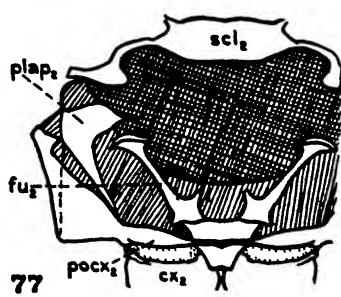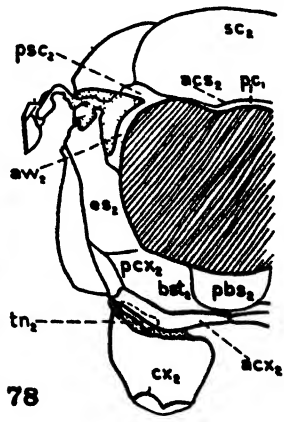
PLATE X

79. Forewing of *Scolops pungens*
80. Hindwing of *Scolops pungens*
81. Forewing of *Tibicina septendecim*
82. Hindwing of *Tibicina septendecim*
83. Forewing of *Lepyronia quadrangularis*
84. Hindwing of *Lepyronia quadrangularis*
85. Forewing of *Aulacizes irrorata*
86. Hindwing of *Aulacizes irrorata*
87. Forewing of *Ceresa bubalus*
88. Hindwing of *Ceresa bubalus*

79   80   81   82   83   84   85   86   87   88
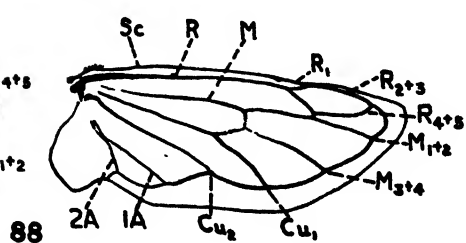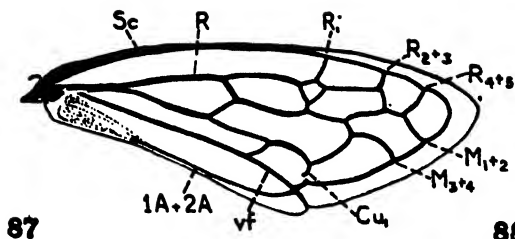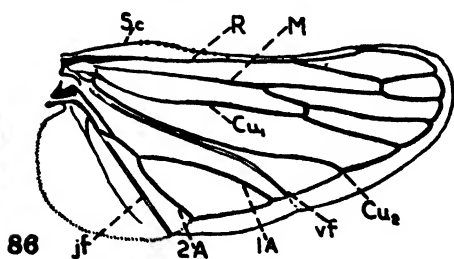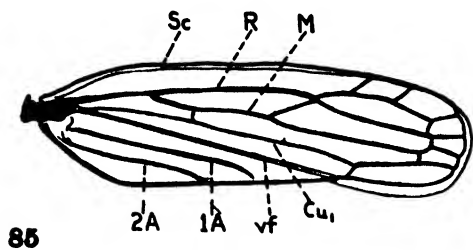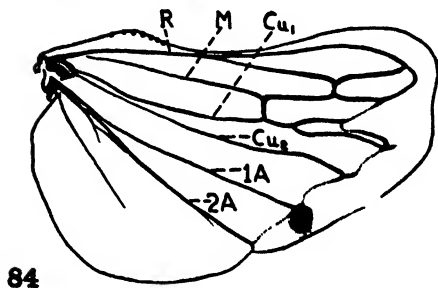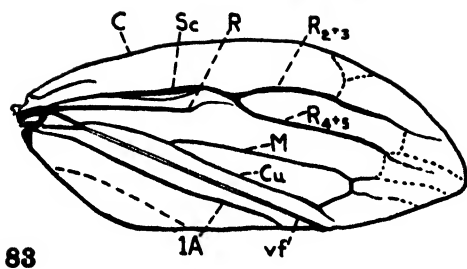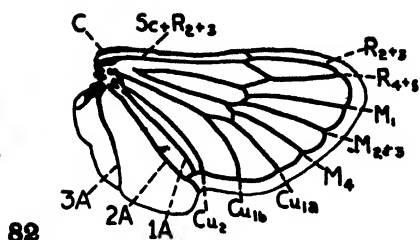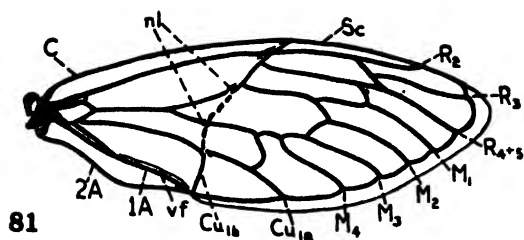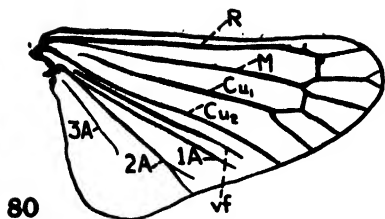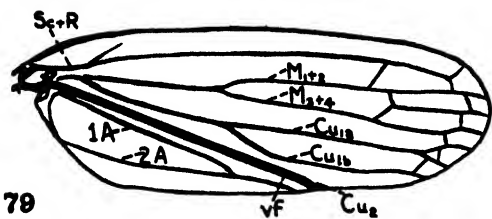
PLATE XI

89. Prothoracic leg of *Scolops pungens*
90. Mesothoracic leg of *Scolops pungens*
91. Metathoracic leg of *Scolops pungens*
92. Tarsal segments and claws of mesothoracic leg of *Scolops pungens*
93. Prothoracic leg of *Tibicina septendecim*
94. Mesothoracic leg of *Tibicina septendecim*
95. Metathoracic leg of *Tibicina septendecim*
96. Tarsal segments and claws of metathoracic leg of *Tibicina septendecim*
97. Prothoracic leg of *Lepyronia quadrangularis*
98. Mesothoracic of *Lepyronia quadrangularis*
99. Metathoracic leg of *Lepyronia quadrangularis*
100. Tarsal segments and claws of mesothoracic leg of *Lepyronia quadrangularis*
101. Prothoracic leg of *Aulacizes irrorata*
102. Mesothoracic leg of *Aulacizes irrorata*
103. Metathoracic leg of *Aulacizes irrorata*
104. Tarsal segments and claws of prothoracic leg of *Aulacizes irrorata*
105. Lateral view of claw of prothoracic leg of *Aulacizes irrorata*

PLATE XIII

105
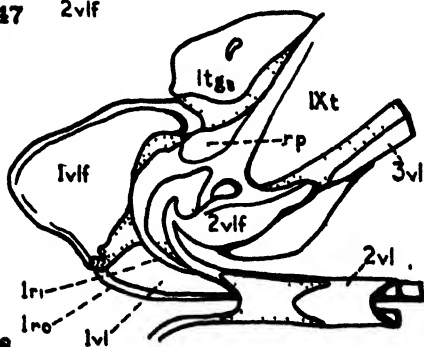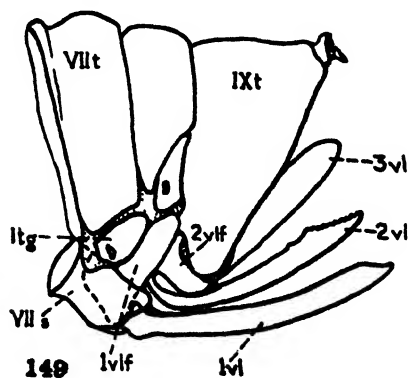
PLATE XIV

107

144

143

145

146

147

148

149

109

PLATE XVI

Ceresa bubalus

150. Caudal view of male genitalia
151. Lateral view of male genitalia
152. Muscles of the male genitalia, lateral view
153. Dissection showing paramere, basal plate, aedeagus, tenth segment, and musculature
154. Ventral view of subgenital plate
155. Caudal view of aedeagus

ILLINOIS BIOLOGICAL
MONOGRAPHS

Volume XX

CONTENTS